

Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism?

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ABSTRACT: Moderate rates of herbivory can enhance primary production. This hypothesis has led to a controversy as to whether such positive effects can result in mutualistic interactions between plants and herbivores. We present a model for the ecology and evolution of plant-herbivore systems to address this question. In this model, herbivores have a positive indirect effect on plants through recycling of a limiting nutrient. Plants can evolve but are constrained by a trade-off between growth and antiherbivore defense. Although evolution generally does not lead to optimal plant performance, our evolutionary analysis shows that, under certain conditions, the plant-herbivore interaction can be considered mutualistic. This requires in particular that herbivores efficiently recycle nutrients and that plant reproduction be positively correlated with primary production. We emphasize that two different definitions of mutualism need to be distinguished. A first ecological definition of mutualism is based on the short-term response of plants to herbivore removal, whereas a second evolutionary definition rests on the long-term response of plants to herbivore removal, allowing plants to adapt to the absence of herbivores. The conditions for an evolutionary mutualism are more stringent than those for an ecological mutualism. A particularly counterintuitive result is that higher herbivore recycling efficiency results both in increased plant benefits and in the evolution of increased plant defense. Thus, antagonistic evolution occurs within a mutualistic interaction.

Keywords: plant-herbivore interaction, nutrient cycling, grazing optimization, evolution, adaptive dynamics, mutualism.

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Can moderate rates of herbivory enhance plant primary production? Such a positive effect of herbivory is proposed by the grazing optimization hypothesis (McNaughton 1979; Hilbert et al. 1981; Dyer et al. 1986). This hypothesis suggests that plant primary production can increase with low grazing intensity and reach an optimum at intermediate grazing before production decreases again when grazing intensity becomes too high. Experimental studies in the Serengeti in Tanzania (McNaughton 1985) and in the La Perouse Bay in Canada (Cargill and Jefferies 1984; Bazely and Jefferies 1989) have demonstrated such increased primary production in plots under herbivory relative to exclosures without herbivores. The relevance of these findings is underlined by theoretical models confirming that, under certain conditions, positive indirect effects of herbivores through nutrient cycling can lead to patterns of grazing optimization (Loreau 1995; de Mazancourt et al. 1998, 1999).

Several authors have even gone further and have suggested that grazing optimization can lead to mutualistic interactions between plants and their herbivores (Owen and Wiegert 1981, 1982; Petelle 1982; Vail 1992), a claim that has attracted much criticism (Silvertown 1982; Belsky et al. 1993; Mathews 1994). According to Belsky et al. (1993, p. 114), no plausible explanation of a real benefit for the individual plant from herbivory has ever been proposed, and “under most ecologically plausible circumstances, selection will favor allocation of plant resources to functions that deter or avoid herbivory, not to those that encourage it.” Since plant defenses diminish the amount of nutrient cycling through the herbivore population, they decrease or prevent the positive indirect effects of herbivory. Therefore, even when herbivory could lead to grazing optimization in principle, optimal plant primary production may never be reached under evolving plant defenses.

Several factors, however, are likely to impede the evolution of maximally efficient plant defense strategies. For example, the synthesis of secondary compounds for plant defense, or the development of specific morphological fea-

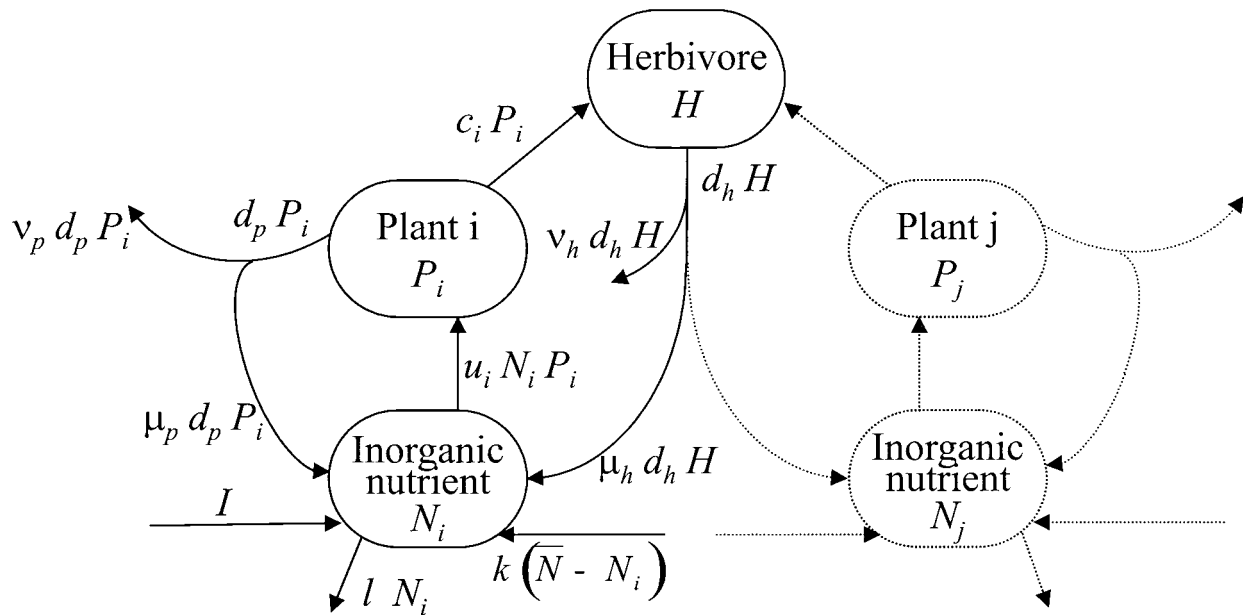


Figure 1: Model for the cycling of a limiting nutrient in an ecosystem comprising plants that are grazed by a generalist herbivore. Plants can employ different strategies; two are shown here, denoted by i and j . Variables and parameters are as defined in table 1.

tures for defense, can divert resources from primary functions within the plant. Trade-offs between growth and defense are likely to result and have been demonstrated in interspecific as well as intraspecific comparisons (van der Meijden et al. 1988; see Herms and Mattson 1992 for a review). With maximum plant defense then being suboptimal, grazing optimization becomes conceivable again, even when taking into account—as demanded by Belsky et al. (1993)—the evolution of plant defenses.

In this article, we investigate the joint evolution of plant primary production and plant defense. Specifically, we consider the effect of trade-offs between the efficacy of plant defense and the uptake rate of a limiting nutrient—the latter being a critical factor affecting plant growth rate. After introducing an ecological model of plant-herbivore interactions based on nutrient cycling (see sections entitled “Nutrient Cycling in Plant-Herbivore Interactions,” “Seasonal Dynamics of Site Occupation,” and “Implications of Frequency-Dependent Selection and Trade-Offs”), we study how evolution within the system is affected by essential characteristics of the nutrient cycle; in particular, we clarify under which ecological conditions plant evolution leads to optimal plant performance (see “Evolution and Optimization of Plant Performance”). To evaluate whether evolved plant-herbivore interactions can be regarded as mutualistic, we distinguish between two different definitions of mutualism based, alternatively, on short-term or long-term assessments. We directly compare

plant performance in the presence and absence of herbivores and show that mutualism between plants and their herbivores is possible under certain conditions (see “Conditions for Plant-Herbivore Mutualism”). These conditions lead to suboptimal plant performance and to the evolution of better-defended plants, implying that mutualistic interactions can occur together with antagonistic evolution. Finally, we evaluate our findings in comparison with previous research (see “Discussion”).

Nutrient Cycling in Plant-Herbivore Interactions

In this section we present a simple model for the open cycle of a limiting nutrient in a plant-herbivore system (see fig. 1; an overview of all variables and parameters used in the model is provided in table 1). Plants with different strategies i differ in their nutrient uptake rate, u_i , and in their herbivore consumption rate, c_i ; other ecological features are assumed not to vary with plant strategy. The herbivore consumption rate c_i is the annual proportion of standing biomass that is removed by herbivory. We assume that plants influence this rate through their level of defense against herbivores.

In keeping with many recent studies that emphasize ecological consequences of spatial heterogeneity (Huston and DeAngelis 1994; Loreau 1996), we do not assume the mineral nutrient pool in the soil to be spatially homogeneous. Instead, plants have nonoverlapping local nutri-

Table 1: Variables and parameters of the model

	Definition (dimension)
Variable:	
P_i	Plant i 's nutrient stock in a site (amount of nutrient per site area)
N_i	Soil mineral nutrient stock in the local pool of a plant i in a site (amount of nutrient per site area)
H	Herbivore nutrient stock per site area (amount of nutrient per site area)
S_i	Fraction of sites occupied by plants of strategy i (dimensionless)
Parameter:	
I	Input of inorganic nutrient in the ecosystem per unit of time and area (amount of nutrient per unit time per site area)
k	Migration rate of nutrient in the soil (per unit time)
l	Loss rate of mineral nutrient (per unit time)
u_i	Plant i 's nutrient uptake rate (per unit time/[amount of nutrient per site area])
c_i	Plant i 's consumption rate (per unit time)
d_p	Plant detritus production rate (per unit time)
μ_p	Fraction of nutrient recycled in the ecosystem along the herbivore pathway (dimensionless)
ν_p	Fraction of nutrient loss for the ecosystem along the plant pathway (dimensionless)
d_h	Herbivore detritus production rate (per unit time)
μ_h	Fraction of nutrient recycled in the ecosystem along the herbivore pathway (dimensionless)
ν_h	Fraction of nutrient lost for the ecosystem along the herbivore pathway (dimensionless)
α	Fraction of plants that die at the end of the season (dimensionless)
Derived variables:	
\bar{N}	Mean stock of soil mineral nutrient in a site (amount of nutrient per site area)
Φ_i	Plant i 's productivity per site area, in terms of the limiting nutrient (amount of nutrient per unit time per site area)
F_i	Seed production of plant i , at the end of the season (number of seeds per site area)

ent depletion zones called “sites,” which are situated around their roots. Each plant absorbs the limiting nutrient from its own local nutrient pool. This spatial heterogeneity prevents direct competitive exclusion (Huston and DeAngelis 1994), which occurs if a single limiting nutrient is provided in a spatially homogeneous nutrient pool (Tilman 1982, 1988). Mineral nutrients can migrate laterally through the soil between nutrient depletion zones through diffusion, transport, or other processes. Model variables and their rates of change are expressed in units of nutrient concentration per site. Each site is occupied by a single plant with a given strategy, and each strategy i occupies a fraction S_i of such sites, so that $\sum_i S_i = 1$.

The following two equations describe the local nutrient dynamics at a site occupied by a plant with strategy i

$$\frac{dN_i}{dt} = I - lN_i + k(\bar{N} - N_i) - u_i N_i P_i + \mu_p d_p P_i + \mu_h d_h H, \quad (1a)$$

$$\frac{dP_i}{dt} = u_i N_i P_i - d_p P_i - c_i P_i, \quad (1b)$$

where N_i is the concentration of mineral nutrient in the soil of a site occupied by a plant with strategy i , and P_i is

the concentration of the limiting nutrient in a plant with strategy i . The accumulation of nutrient in the herbivore population per site is described by

$$\frac{dH}{dt} = \sum_i S_i c_i P_i - d_h H, \quad (1c)$$

where H is the concentration of the limiting nutrient accumulated in the herbivore population per site. Herbivores are assumed to be distributed uniformly across all sites of the system. The primary production of plants of strategy i is measured by their rate of nutrient uptake,

$$\Phi_i = u_i N_i P_i. \quad (2)$$

In the following four paragraphs we explain in detail how to interpret the various terms in equations (1).

The boundaries of the ecological system are open to nutrient flows: we assume a constant input of nutrient (in inorganic form) into all sites at rate I . At each site, mineral nutrient is lost at rate l . Nutrient concentrations in the soil are also altered by nutrient diffusion between sites: inflows of nutrient to a local pool are proportional to the difference between the mean and the local nutrient concentration, $\bar{N} - N_i$ (negative values represent outflows),

and to the nutrient diffusion coefficient in the soil, k . The first assumption is based on a spatially homogeneous mixture of different plant strategies across sites. The mean nutrient concentration is $\bar{N} = \sum_i S_i N_i$.

Plants absorb nutrients at a rate that is proportional to their nutrient uptake rate u_p , the local soil concentration N_p , and the amount of nutrient P_i within the plant, which we assume to be proportional to plant biomass. Nutrient stored in plants can be recycled through two different pathways, which we call the plant pathway and the herbivore pathway (fig. 1). Nutrient not consumed by the herbivore follows the plant pathway. Each plant produces detritus at a rate d_p . As we are only interested in ecological steady states, time-delayed detritus dynamics have no consequences (de Mazancourt et al. 1998) and therefore are not considered here. A proportion μ_p of nutrient in plant detritus is mineralized and retained in the local nutrient pool around the plant. The rest, that is, a fraction $\nu_p = 1 - \mu_p$, accumulates as resistant organic matter or is lost and leaves the ecosystem through leaching, volatilization, or other processes. Recycling of plant nutrient in the soil thus occurs at a rate that is proportional to the plant's recycling fraction pathway μ_p , the plant detritus production rate d_p , and the amount of nutrient P_i within the plant. Plant pathway's recycling fraction is likely to depend not only on the plant's environment, soil, and microbial fauna but also on characteristics of the plant's species (de Mazancourt and Loreau 2000a).

Nutrients consumed by herbivores follow the herbivore pathway. Although more complicated assumptions could readily be made, here we study the simple case of a donor-controlled herbivory: the proportion of standing biomass consumed by herbivores then does not depend on the density of herbivores. In previous work, we have shown that other forms of herbivory give the same results as donor-controlled herbivory, on an ecological timescale. The resulting model, however, was much more complicated and difficult to interpret (de Mazancourt et al. 1998). We therefore focus here on the simple case where herbivore consumption rate is proportional to the amount P_i of nutrient within the plant and the rate c_i of plant consumption by herbivores.

Herbivore detritus is not explicitly represented in the model: as for plant detritus, we assume that it is immediately mineralized. While a fraction, μ_h , of herbivore nutrient is recycled to the soil, the remaining fraction $\nu_h = 1 - \mu_h$ leaves the ecosystem or accumulates as resistant organic matter. Recycled nutrient is uniformly distributed among sites, as would result if the herbivore is highly mobile. This is a conservative assumption: if herbivores are sedentary and recycling occurs primarily on the least-defended plant type, evolution of less-defended plants is favored (de Mazancourt and Loreau 2000b). Note

that any detritus that herbivores distribute outside the sites considered in the model amounts to a loss of nutrient from the system and therefore ought to be accounted for in the fraction ν_h of lost nutrients. Analogously to plant nutrient, recycling of herbivore nutrient to the soil occurs at a rate proportional to the herbivore pathway's recycling fraction μ_h , the rate of herbivore detritus production d_h , and the amount H of nutrient within the herbivore population.

Equations (1) specify the nutrient dynamics within a season. As a basis for the subsequent evolutionary analyses, we now consider the ecological dynamics between seasons.

Seasonal Dynamics of Site Occupation

At the beginning of each growth season, a fraction α of plants die, and the vacant sites are recolonized. Colonization success of different plant strategies depends on their relative contributions to the plant population's seed pool; a plant with strategy i contributes F_i seeds to this pool. The fraction of sites occupied by plant strategy i in the next season is then given by

$$S_i(t+1) = (1 - \alpha)S_i(t) + \alpha \frac{S_i(t)F_i(t)}{\sum_j S_j(t)F_j(t)}. \quad (3)$$

Within a season, the number of sites occupied by each strategy does not change. However, the plants grow during the season. At the end of the season, the number of sites occupied by each strategy is updated according to equation (3).

We assume that the duration of seasons is sufficiently long for nutrient concentrations to attain their equilibria. This might appear as a constraining assumption, but it only requires that the model parameters be carefully chosen to match the seasonal timescale (de Mazancourt et al. 1998). For example, the state of a compartment such as soil resistant organic matter, with a very long resident time compared with the timescale of the season, can be considered as constant during one season.

For the plant seed production F_i , we consider two alternative scenarios: either seeds are produced in proportion to plant biomass, measured by the amount of nutrient in the plant, $F_i \propto P_i^*$, or seed production is proportional to plant primary production, measured by the rate of nutrient absorption, $F_i \propto \Phi_i^*$, where the asterisk indicates an equilibrium value. These seed production scenarios should be regarded as two extremes along a spectrum of possible dependencies. Both alternatives are underpinned by clear ecological motivations. On the one hand, the amount of nutrient in the plant is positively correlated with plant standing biomass; it is this biomass that can be reallocated

to seed production at the end of each season. Such a scenario is likely for an annual plant ($\alpha = 1$). On the other hand, the amount of nutrient that a plant absorbs per unit time is positively correlated with plant primary production and characterizes the amount of resources that plants can continuously divert to seed production during the season. Such a scenario is likely to hold for perennial plants ($\alpha < 1$) and corresponds to classical physiological allocation models, describing the pattern of resource allocation between different functions (Mole 1994). The two scenarios are similar in assuming a constant allocation of plant resources to the production of seeds and vegetative biomass; for the sake of simplicity, we do not explore the consequences of a trade-off between these two functions. Also, both scenarios result in a positive correlation between seed production and plant biomass, which is observed in many empirical studies (Aarssen and Taylor 1992).

We consider the two seed production scenarios introduced here as useful starting points; in appendix A, we show that intermediate cases, in which seed production is proportional to a linear combination of plant biomass and primary production, lead to evolutionary outcomes that lie in between the outcomes for the two “pure” cases. Our two simple cases therefore cover a wider range of options.

Implications of Frequency-Dependent Selection and Trade-Offs

For predicting which plant strategy is selected for in our model, we need to account for frequency-dependent selection: the reproductive rate of a plant does not only depend on its own strategy but also on those of all other plants in the system. Specifically, its reproduction depends on herbivore density and nutrient inflow through the soil, both of which are affected by the strategies of all other plants in the system. If, for example, other plants allocate a high fraction of their resources to defense, a plant with weak defense is expected to experience a particularly high selection pressure toward stronger defense.

The theory of adaptive dynamics (Dieckmann and Law 1996; Metz et al. 1996; Dieckmann 1997; Geritz et al. 1998), which we use here to study the joint evolution of nutrient uptake and defense, takes into account frequency dependence. An exhaustive study of evolutionary outcomes in the model introduced above is not the focus of this article; such a systematic analysis, using adaptive dynamics, is presented elsewhere (de Mazancourt 1998; C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript).

Natural populations of plants can neither increase their nutrient uptake rate indefinitely, nor completely avoid consumption by herbivores. We therefore assume that

plant evolution is confined between two extreme strategies: at one extreme, plants maximize the efficiency of their antiherbivore defense system, resulting in a strategy D with a minimum rate of herbivory and a minimum nutrient uptake rate, $D = (c_{\min}, u_{\min})$; at the other extreme, they maximize the efficiency of their nutrient uptake system, resulting in a strategy U with a maximum nutrient uptake rate and a maximum herbivore consumption rate, $U = (c_{\max}, u_{\max})$. Intermediate plant strategies (c, u) are confined on a trade-off curve. This trade-off reduces the originally two-dimensional strategy space (c, u) of plants to a single dimension so that we can characterize each plant strategy by its herbivore consumption rate c (see appendix B).

In the following sections, we focus attention on trade-offs that result in continuously stable strategies, or CSSs (Eshel and Motro 1981; Eshel 1983). A CSS has two independent properties. First, it is convergence stable in the sense of Christiansen (1991): for a given resident strategy, only mutants closer to the convergent-stable strategy can invade, that is, the evolutionary dynamics converge toward this strategy. Second, it is evolutionarily stable in the sense of Maynard Smith (Maynard Smith and Price 1973; Maynard Smith 1982): when the strategy is resident, it cannot be invaded by any other mutant strategy. An evolutionarily stable strategy, once attained, is an endpoint of the evolutionary process, and the property of convergence stability ensures that this evolutionary endpoint can be reached. It can be shown that, for the model considered here, evolutionarily and convergence-stable outcomes are expected for realistic parameter values (de Mazancourt 1998; C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript).

Evolution and Optimization of Plant Performance

In this section, we explore the implications of evolution for plant performance. We investigate how essential characteristics of the nutrient cycle affect the strategy favored by evolution and whether this strategy coincides with the one that maximizes primary production or plant biomass. In other words, can optimal plant biomass or primary production be reached under evolving plant defenses? To assess this question, which lies at the heart of the grazing optimization controversy, we compare the CSSs for each seed production scenario (proportional to plant biomass or to primary production) with the two strategies that maximize plant biomass or primary production.

Figure 2 shows the relative positions of the four strategies; the method used for obtaining these results is outlined in appendix B. The various cases depicted in figure 2 illustrate the influence of different model parameters. In particular, the effects of the fraction of nutrient recycled

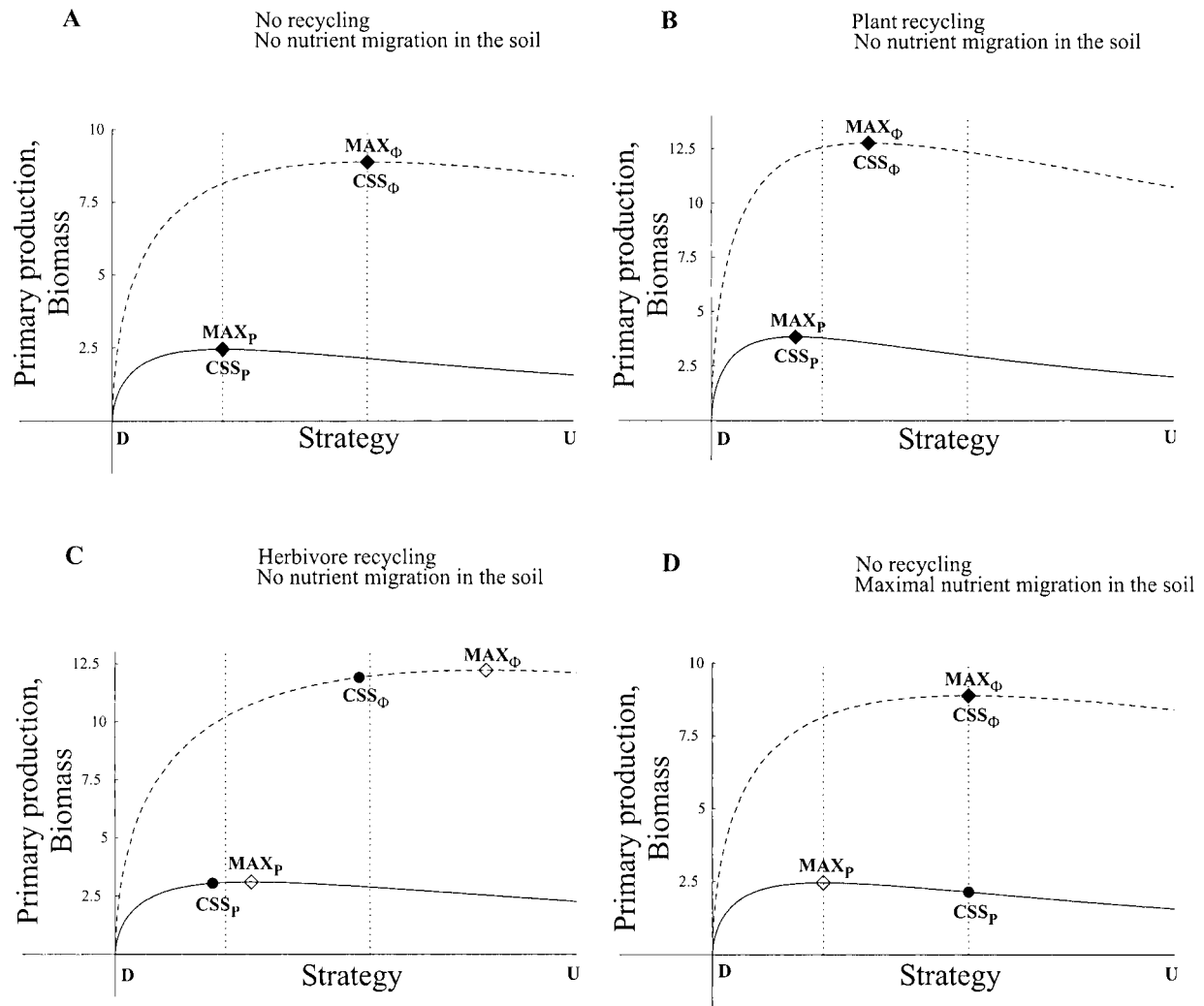


Figure 2: Biomass (solid line) and primary production (dashed line) as a function of plant strategies, ranging from the maximally defended plant strategy D to the minimally defended strategy U that allocates most resources to nutrient uptake. Evolutionary outcomes (continuously stable strategies) are CSS_p (seed production proportional to plant biomass) and CSS_ϕ (seed production proportional to primary production). MAX_p is the strategy that maximizes plant biomass, and MAX_ϕ maximizes primary production. *A*, No migration of nutrient in the soil, and no plant or herbivore nutrient recycling. For comparison, strategies MAX_p and MAX_ϕ resulting for this baseline case are indicated by dotted lines and repeated unaltered in the three other panels. *B*, Effect of plant nutrient recycling. *C*, Effect of herbivore nutrient recycling. *D*, Effect of migration of nutrient in the soil (shown for an infinite migration rate k of nutrient in the soil). Parameters: $I = 28.11 \text{ kgN} \times \text{ha}^{-1} \times \text{yr}^{-1}$; $l = 1.80 \text{ yr}^{-1}$; $d_p = 2.15 \text{ yr}^{-1}$. Trade-off function: $c_{\min} = 0.54 \text{ yr}^{-1}$; $c_{\max} = 3.20 \text{ yr}^{-1}$; $u_i = 0.17 + 0.17(c_i - c_{\min})^{0.63} \text{ ha} \times \text{kgN}^{-1} \times \text{yr}^{-1}$. *A*, $\nu_p = \nu_h = 1$; $k = 0 \text{ yr}^{-1}$. *B*, $\nu_p = 0.46$; $\nu_h = 1$; $k = 0 \text{ yr}^{-1}$. *C*, $\nu_p = 0.95$; $\nu_h = 0.72$; $k = 0 \text{ yr}^{-1}$. *D*, $\nu_p = \nu_h = 1$; $k = 1,000,000 \text{ yr}^{-1}$.

along the plant pathway, the fraction of nutrient recycled along the herbivore pathway, and the migration rate of nutrient in the soil are demonstrated.

Let us first focus on how the two maximizing strategies are affected by varying model parameters. Consumption has a greater impact on plant biomass than it has on primary production because consumption affects soil nutrient concentration N such that, at equilibrium, $\Phi_i^* = u_i N_i^* P_i^* = (d_p + c_i) P_i^*$. Consequently, maximizing biomass

always requires a smaller consumption rate than does maximizing primary production (fig. 2A–2D). Recycling of plant detritus shifts the maximizing strategies toward better-defended plants (cf. fig. 2A and 2B). This is because a smaller consumption increases the nutrient conservation in the system, as plant nutrient flows through the plant pathway. Recycling of herbivore detritus shifts the maximizing strategies toward less-defended plants (cf. fig. 2A and 2C): because herbivore detritus is recycled whereas

plant detritus is not, here it is the greater consumption of plants by herbivores that improves conservation of nutrient in the system. Migration of nutrient in the soil does not change the positions of the two maximizing strategies, since it does not influence biomass and production in a monoculture, in which the mean and the local nutrient concentrations in the soil are equal.

We can now compare the results of the previous paragraph with the effect model parameters have on the position of the CSSs. When plant recycling occurs, but both herbivore recycling and migration of mineral nutrient are absent, evolution simply leads toward those strategies that maximize biomass or primary production, depending on the scenario used for seed production (cf. fig. 2A and 2B). However, two factors—herbivore recycling and migration of mineral nutrient—can cause the CSSs to depart from the corresponding maximizing strategies by giving more importance either to defense or to nutrient uptake. Herbivore recycling alone favors plants that are better defended: better-defended plants benefit from nutrient recycled through herbivory on neighboring plants, while also incurring a lower cost from herbivory and, thus, can invade less-defended plants (cf. fig. 2A and 2C). For CSSs resulting from the primary production scenario this effect is proportional to plant recycling. Migration of mineral nutrient in the soil selects for plants with the best capability of local nutrient depletion: they benefit from the nutrient flow from neighboring rooting zones. This leads to selection for plants with higher nutrient uptake rates (cf. fig. 2D and 2A–2C). Evolution then leads toward the same strategy that maximizes primary production when no recycling occurs (cf. fig. 2D and 2A) because this strategy minimizes losses of soil inorganic nutrient. Intermediate cases lie between the extreme situations discussed above.

It is interesting to note that all the patterns described in figure 2 are general and, in the presence of a CSS, apply irrespective of any specific assumptions regarding the trade-off curve.

Conditions for Plant-Herbivore Mutualism

So far we have shown that plant evolution does not always maximize primary production or biomass. Remarkably, the same parameter that can enhance primary production in the presence of herbivores—the fraction of nutrient recycled along the herbivore pathway—leads to suboptimal plant performance through the evolution of plant defense. Despite being suboptimal, however, evolution could still lead to mutualistic interactions, as suggested by several authors (Owen and Wiegert 1981, 1982; Petelle 1982; Vail 1992).

The classical method for identifying mutualistic ecological interactions is based on removal experiments or press perturbations (Schoener 1983; Bender et al. 1984; Krebs 1985);

if each of the two populations decreases in performance (i.e., in density, biomass, or production) after the other population with which it interacts has been removed or is kept at low densities, the interaction is considered to be mutualistic.

In spite of the heuristic value of such a definition, its practical application requires careful consideration of several details. First, responses to different measures of performance may not always point toward the same conclusion. Second, results can be qualitatively affected by the strength of perturbations. Third, the short- and long-term effects of a removal should be distinguished: while the former reflects the ecological response of a system, the latter also accounts for any potential evolutionary change resulting from a perturbation (Douglas and Smith 1989; Law and Dieckmann 1998). This leads to two different definitions of mutualism: we refer to these as ecological and evolutionary mutualisms, respectively (C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript). For an ecological mutualism, the performance of partners is evaluated before any evolution can occur, whereas for an evolutionary mutualism, the mutual benefit has to remain (or arise) after adaptation to the removal has taken place. The beneficial effect of plants on herbivores is straightforward and needs no further consideration. We investigate the potentially beneficial effect of herbivores on plants by model-based herbivore removal experiments that allow us to compare plant performances with and without herbivores over short and long time spans (fig. 3).

In the presence of herbivores, equilibrium biomass and primary production of a monomorphic population with strategy $(c_{\text{CSS}}, u_{\text{CSS}})$ are given by, respectively,

$$P_{\text{CSS}}^* = \frac{I - l(d_p + c_{\text{CSS}})/u_{\text{CSS}}}{\nu_p d_p + \nu_h c_{\text{CSS}}}, \quad (4a)$$

$$\Phi_{\text{CSS}}^* = (d_p + c_{\text{CSS}})P_{\text{CSS}}^*. \quad (4b)$$

Starting from the evolutionarily stable situation $(c_{\text{CSS}}, u_{\text{CSS}})$, we can determine the short-term response of the plant population to the removal of herbivores: biomass and primary production in the postremoval ecological equilibrium are given by

$$P_{\text{eco}}^* = \frac{I - l d_p / u_{\text{CSS}}}{\nu_p d_p}, \quad (5a)$$

$$\Phi_{\text{eco}}^* = d_p P_{\text{eco}}^*. \quad (5b)$$

By comparing equations (4) and (5), we see that in the short-term response to herbivore removal, plant biomass is always increased and primary production is decreased if

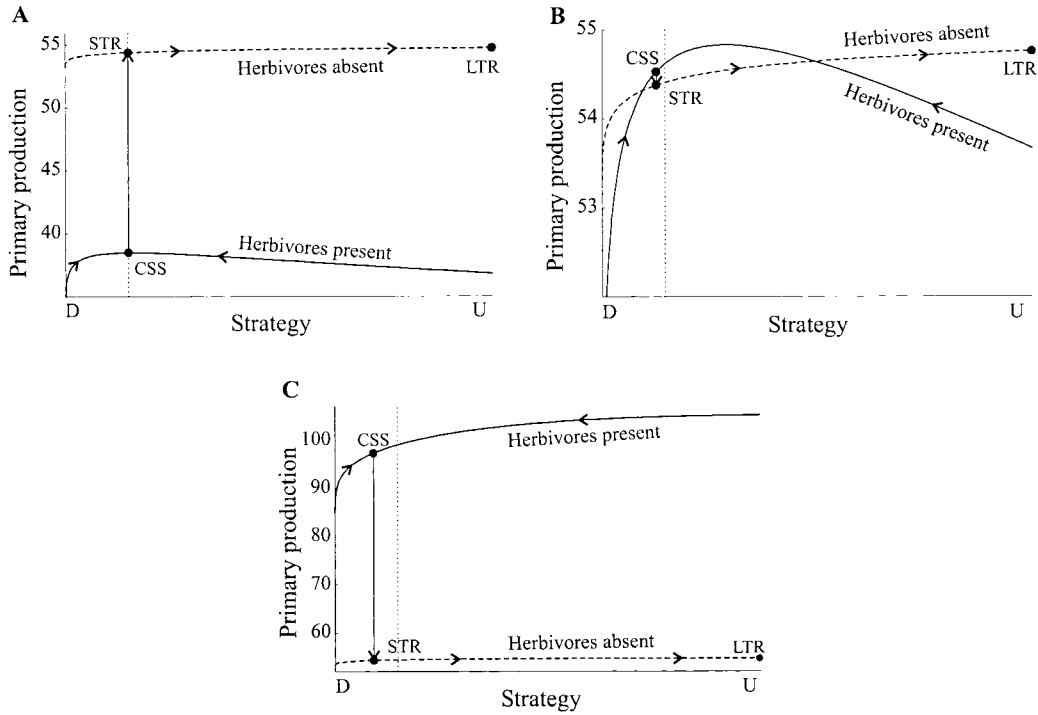


Figure 3: Primary production along the trade-off curve of plant strategies in the presence of herbivores (*solid line*) and in their absence (*dashed line*). When herbivores are present, evolution leads to a continuously stable strategy (CSS). To test whether plant-herbivore interactions are mutualistic, we compare plant performance in the presence and absence of herbivores. Two different plant responses need to be distinguished: in the short-term response (*STR*), herbivores have been removed but plants have not yet adapted to the herbivore-free situation; in the long-term response (*LTR*), herbivores have been removed and plants have had time to adapt. *A*, No mutualism: plant performance is always decreased in the presence of herbivores. *B*, Ecological mutualism: plant performance is decreased by the short-term response to herbivore removal (*STR* is lower than *CSS*). However, on the long term, the removal leads to an increase in primary production (*LTR* is higher than *CSS*), and there is no evolutionary mutualism. *C*, Ecological and evolutionary mutualism: herbivore removal results, on the short term and on the long term, in decreased plant performance (*CSS* higher than *STR* and *LTR*). In all three panels, the dotted line shows the *CSS* for case *A* to facilitate comparison between panels. Parameters: $I = 39.77 \text{ kgN} \times \text{ha}^{-1} \times \text{yr}^{-1}$; $l = 4.57 \text{ yr}^{-1}$; $k = 0.47 \text{ yr}^{-1}$; $d_p = 0.57 \text{ yr}^{-1}$; $v_p = 0.72$. Trade-off function: $c_{\min} = 2.85 \text{ yr}^{-1}$; $c_{\max} = 8.27 \text{ yr}^{-1}$; $u_i = 1.88 + 2.75 (c_i - c_{\min})^{0.43} \text{ ha} \times \text{kgN}^{-1} \times \text{yr}^{-1}$. *A*, $v_h = 0.95$. *B*, $v_h = 0.636$. *C*, $v_h = 0.30$.

nutrient loss along the herbivore pathway is sufficiently smaller than along the plant pathway

$$v_h/v_p < 1 - \frac{(d_p + c_{\text{CSS}})/u_{\text{CSS}}}{I/l - d_p/u_{\text{CSS}}}. \tag{6a}$$

A necessary (but not sufficient) condition for inequality (6a) to be fulfilled is that its right-hand side be positive: the nutrient input into the system has to exceed a threshold value

$$I/l > \frac{2d_p + c_{\text{CSS}}}{u_{\text{CSS}}}. \tag{6b}$$

We can thus conclude that herbivore removal always has a positive short-term effect on plant biomass. It also has a positive short-term effect on primary production, unless

inequality (6a) is fulfilled, that is, unless nutrient recycling is sufficiently more efficient along the herbivore pathway than along the plant pathway. Inequalities (6a) and (6b) are thus the prerequisites for grazing optimization to occur.

We now extend the preceding analysis to encompass the plants' evolutionary response to herbivore removal. Without herbivores, plants should not allocate any resources to defense and, therefore, evolve toward the strategy with maximal uptake rate u_{max} . The biomass and primary production after herbivore removal and plant evolution are thus:

$$P_{\text{evo}}^* = \frac{I - ld_p/u_{\text{max}}}{v_p d_p}, \tag{7a}$$

$$\Phi_{\text{evo}}^* = d_p P_{\text{evo}}^*. \tag{7b}$$

By comparing equations (5) and (7) we see that evolution

after herbivore removal always leads to increased plant biomass and primary production, $P_{\text{evo}}^* > P_{\text{eco}}^*$ and $\Phi_{\text{evo}}^* > \Phi_{\text{eco}}^*$. Comparing equations (4) and (7) shows that the long-term response to herbivore removal always increases plant biomass relative to the evolutionary equilibrium attained in the presence of herbivores, $P_{\text{evo}}^* > P_{\text{CSS}}^*$. Also, primary production after herbivore removal and plant evolution is lower than at the preremoval CSS, $\Phi_{\text{evo}}^* < \Phi_{\text{CSS}}^*$, if

$$\nu_h/\nu_p < 1 - \left(\frac{d_p + c_{\text{CSS}}}{c_{\text{CSS}}} \right) \left[\frac{(d_p + c_{\text{CSS}})/u_{\text{CSS}} - d_p/u_{\text{max}}}{II - d_p/u_{\text{max}}} \right]. \quad (8a)$$

Again, this condition can only be fulfilled if its right-hand side is positive, that is,

$$II > \frac{2d_p + c_{\text{CSS}} + (1 - u_{\text{CSS}}/u_{\text{max}})d_p^2/c_{\text{CSS}}}{u_{\text{CSS}}}. \quad (8b)$$

After herbivore removal, primary production either increases (if $u_{\text{CSS}} < u_{\text{max}}$) or remains constant (if $u_{\text{CSS}} = u_{\text{max}}$). This implies that $\Phi_{\text{evo}}^* \geq \Phi_{\text{eco}}^*$ and that inequalities (8) are therefore more restrictive than inequalities (6).

We thus conclude that herbivore removal has a positive effect on plant biomass in the short term, and even more so in the long term. Removal also has a positive effect on primary production if herbivores are not sufficiently efficient at recycling nutrient (see inequalities [6a] and [8a]). If, however, nutrient loss via the herbivore pathway is sufficiently smaller than via the plant pathway, herbivore removal results in a loss of plant performance in terms of primary production. In other words, if herbivores contribute enough to nutrient conservation, both the short-term and long-term responses to herbivore removal can indicate a plant-herbivore mutualism. The conditions for an ecological mutualism turn out to be less stringent than those for an evolutionary mutualism. Yet, in the range of parameters explored, these two conditions appear to be only marginally different. Figure 3 shows primary production and plant-herbivore interaction in three cases of herbivore recycling efficiency. In figure 3A, herbivore recycling efficiency is too low and the interaction is exploitative. In figure 3B, the interaction is an ecological mutualism but not an evolutionary mutualism. In figure 3C, herbivore recycling efficiency is sufficiently high for the interaction to be both an ecological and an evolutionary mutualism. Conditions for mutualism depend on the model parameter in a more complex way than inequalities (6) and (8) might suggest: both uptake and consumption at the CSS depend on the model parameters.

It is instructive to understand the shape of the curves shown in figure 3. In the absence of herbivores, both biomass and primary production increase along the trade-off

curve: as plant nutrient uptake increases, nutrient loss through leaching decreases. In the presence of herbivores, two factors must be taken into account. The first effect results from herbivory: biomass always decreases with the consumption rate as long as herbivores induce some nutrient loss from the system ($\nu_h > 0$); primary production increases if the herbivore recycling efficiency is larger than the fraction of nutrient recycled along the plant pathway. The second effect results from leaching: depending on the shape of the trade-off, leaching can either increase or decrease along the trade-off curve; this results, respectively, in decreased or increased biomass and primary production. In the example featured in figure 3, leaching presents a humped shape along the trade-off, which results in a humped shape for primary production. While the analysis in this section is based on a donor-controlled herbivory, preliminary results for recipient-controlled Lotka-Volterra interactions point to identical conclusions.

Discussion

We now evaluate our findings in the light of various hypotheses and ongoing controversies concerning the evolutionary ecology of plant-herbivore interactions.

The Grazing Optimization Controversy: Can Evolution Lead to Plant-Herbivore Mutualism?

In “Conditions for Plant-Herbivore Mutualism” we have seen how to distinguish between the short-term and long-term consequences of removal experiments. Both alternative perspectives lead to useful definitions of mutualism: interactions are mutualistic in the ecological sense if removal results in a short-term loss of performance; they are mutualistic in the evolutionary sense when this loss occurs in the long term (fig. 3). In the latter case, we can think of a population adapting after the removal of its mutualistic partner, but the evolutionary perspective is equally relevant when considering a situation before the two partners first came into close ecological contact.

While the two definitions of mutualism may lead to the same conclusion, results of these independent assessments may also challenge each other. Of particular interest to this discussion is the case when interactions are mutualistic in the ecological but not in the evolutionary sense. To characterize this combination, Douglas and Smith (1989) have introduced the notion of evolved dependence, which they contrast with that of evolutionary benefit. The former may merely reflect the evolutionary consequences of a past history of tight ecological interaction, and may vanish once the association is lost. For example, during association and evolution with a herbivore, and due to some side effects of herbivory, a plant may have lost its ability to perform

well in the absence of that herbivore, making it dependent on its exploiter (fig. 3B).

Some plants have been shown to overcompensate for herbivory (i.e., they produce more seeds when grazed). For these plants, herbivory releases apical dominance, and grazed plants therefore produce more tillers and more seeds than ungrazed plants (Paige and Whitham 1987; Lennartsson et al. 1997, 1998; Paige 1999; Strauss and Agrawal 1999; C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript). One explanation of this effect may be that, in the course of its evolutionary history with the herbivore, the plant has evolved a mechanism by which reserves are stored and mobilized when the risk of herbivory is over (Nilsson et al. 1996a, 1996b). This mechanism is advantageous in the presence of the herbivore but not in its absence: the plant has evolved a dependence on the herbivore. An evolutionary benefit, on the other hand, only occurs when interactions are mutualistic both in the ecological and in the evolutionary sense (fig. 3C).

We have seen in the previous section that when plant seed production is proportional to plant biomass, herbivore removal has a positive short-term and long-term effect on plant biomass and, hence, on plant seed production. The effect of herbivores on plants is then always exploitative. However, when plant fecundity is proportional to primary production, and if the nutrient input to the system is sufficient so that inequalities (6a) and (8a) can be fulfilled, increasing the efficiency of nutrient recycling by herbivores leads to mutualistic plant-herbivore interactions (fig. 3). At low levels of herbivore recycling efficiency, the interaction is exploitative (fig. 3A). But when herbivore recycling efficiency is increased to intermediate levels, the plant-herbivore interaction becomes mutualistic from an ecological point of view (fig. 3B). Yet, plants do not benefit from herbivores but may rather have evolved a dependence on them. Eventually, when herbivores recycle nutrient with a high efficiency, the plant-herbivore interaction becomes mutualistic in the evolutionary sense and plants truly benefit from herbivores (fig. 3C).

Distinguishing between ecological and evolutionary mutualisms, with the associated concepts of evolved dependence and evolutionary benefit, is of particular relevance in the context of the grazing optimization controversy (C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript). Although some authors (Douglas and Smith 1989; Belsky et al. 1993; Tuomi et al. 1994; Järemo et al. 1999) appear to be willing to adopt an evolutionary definition of mutualism, it is evident from the results presented here that this perspective is more restrictive than the corresponding ecological definition.

Are Mutualistic Plant-Herbivore Interactions Likely to Occur in Nature?

We have shown in this article that plant-herbivore mutualism can occur if, first, the fraction of nutrients recycled through the herbivore pathway is sufficiently higher than the fraction of nutrients recycled through the plant pathway and, second, plant reproduction is proportional to primary production, or at least sufficiently dependent on it (appendix A). de Mazancourt et al. 1999 discussed the likelihood that the first condition could be met. That study shows that herbivory is likely to lead to improved conservation of nutrients in some ecosystems. The specific example we considered is a savanna ecosystem, where fires volatilize nearly all the nitrogen remaining in plant standing biomass at the end of each season. Herbivores can promote nutrient conservation in such a system by reducing plant standing biomass.

The current literature does not yet allow evaluating the likelihood that the second condition could be met. A primary reason for this state of affairs lies in the fundamental difficulties associated with measuring primary production, especially in the presence of herbivores. Therefore, most experiments measure plant reproduction as a function of plant standing biomass and do not permit discrimination between the two hypothetical scenarios of seed production considered here. Yet, it seems very likely that plant reproduction depends on both standing biomass and uptake fluxes. As shown in appendix A, intermediate scenarios of seed production can also result in mutualistic interaction, although conditions then are more stringent.

Nutrient Cycling and Plant-Herbivore Mutualism

This model shows that, if plant defense is costly, plants might be “forced” into a mutualistic interaction with their herbivores: although one component of the selection pressure favors ever-improving defenses, this process is stopped by the cost of such defense strategies.

In a different model (de Mazancourt and Loreau 2000b), we showed another process that might lead to the evolution of plant-herbivore mutualism: spatial heterogeneity of the interaction. If recycling occurs primarily beneath plants preferred by the herbivore, as would occur for small sedentary herbivores like caterpillars, it is primarily those plants that benefit from nutrient recycling along the herbivore pathway. Under such conditions, mutualism can occur more easily. In the present model, taking into account the spatial heterogeneity of the interaction would drive evolutionary outcomes closer to the strategy that maximizes primary production or biomass and would thus make the conditions for mutualism less stringent.

Belsky's Argument: Antagonistic versus Mutualistic Coevolution

In her 1986 article (p. 885), Belsky asked whether grasses and their grazers have coevolved mutualistically. Observing the numerous antiherbivore defenses that grasses have evolved, she then concluded that “indisputably..., these adaptations suggest an antagonistic relationship, not a mutualistic one.”

In the model presented in this article, mutualistic interactions between plants and their herbivores may arise when herbivores are sufficiently more efficient at recycling nutrient than are plants. As described above, increasing nutrient recycling by herbivores can result in more and more mutualistic plant-herbivore interactions (fig. 3). Notice, however, that along the same gradient of recycling efficiency there is selection toward increased levels of plant defense at the expense of reduced nutrient uptake (figs. 2A, 2C, 3). This results from the fact that defended strategies benefit from herbivore recycling and yet suffer less consumption by herbivores; such strategies are therefore selected when herbivore recycling increases. Surprisingly, the increase of plant defense against herbivores may go hand in hand with the build up of mutualistic plant-herbivore interactions. Although this finding may seem paradoxical at first sight, such evolutionary conflicts between partners are well known to exist in mutualistic interactions (Anstett et al. 1997; Law and Dieckmann 1998; Hibbett et al. 2000; van Baalen and Jansen, in press): mutualism can arise even though one partner evolves enhanced defenses. In other words, antagonistic evolution can occur within a mutualistic interaction. This shows that the question whether plant-herbivores interactions are mutualistic or antagonistic (Belsky 1986; Järemo et al. 1999) can be misleading. Antagonism refers to an interaction where two forces of selection are in opposition (Pianka 1974), and this notion does not address the net effect of the interaction on the fitness of individuals. We propose to classify a plant-herbivore interaction as exploitative when it is not mutualistic (C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript).

The investigations of plant responses to herbivory presented in this article are rooted in a description of nutrient cycling and link the physiological, ecological, and evolutionary aspects of plant-herbivore interactions. Tying together these different aspects of ecological research into an integrated perspective allows us to consider the evolutionary consequences of ecological interactions and the ecological implications of evolutionary change.

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APPENDIX A

Seed Production as a Linear Combination of Plant Biomass and Primary Production

In this appendix we show that if seed production is a linear combination of plant biomass and primary production, the evolutionary outcome is intermediate between these

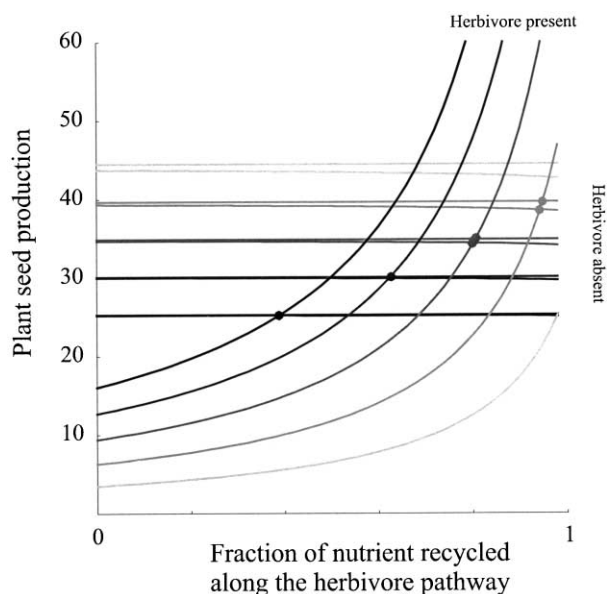


Figure A1: Plant seed production as a function of the fraction of nutrient recycled along the herbivore pathway in the presence and in the absence of herbivores and for different scenarios of seed production: from light gray to black, $F = P^*$, $F = (3/4)P^* + (1/4)\Phi^*$, $F = (1/2)P^* + (1/2)\Phi^*$, $F = (1/4)P^* + (3/4)\Phi^*$, and $F = \Phi^*$. Two sets of curves (labeled in the figure) show seed production in the presence and absence of herbivores. For the latter case, we distinguish between seed production before (*lower curve*) and after (*upper curve*) evolutionary adaptation to this absence. Plant-herbivore interaction is mutualistic whenever plant seed production is higher in the herbivore's presence than in its absence. For each scenario, dots show the threshold condition for the interaction to be an ecological (*lower dot*) or an evolutionary mutualism (*upper dot*); the interaction is mutualistic to the right of the dots. In the example shown, the interaction can be mutualistic when seed production is proportional to primary production (*black curves*) but not when seed production proportional to biomass (*lightest curves*). This figure demonstrates that intermediate scenarios of plant seed production can lead to mutualistic interactions. Parameters: $I = 19.77 \text{ kgN} \times \text{ha}^{-1} \times \text{yr}^{-1}$; $l = 4.57 \text{ yr}^{-1}$; $k = 8.47 \text{ yr}^{-1}$; $d_p = 0.57 \text{ yr}^{-1}$; $v_p = 0.77$. Trade-off function: $c_{\min} = 2.85 \text{ yr}^{-1}$; $c_{\max} = 7.27 \text{ yr}^{-1}$; $u_i = 0.58 + 3.64(c_i - c_{\min})^{0.55} \text{ ha} \times \text{kgN}^{-1} \times \text{yr}^{-1}$.

two extreme cases. In general, the evolutionary outcome is determined by the shape of the trade-off curve relative to the invasion boundaries of strategies that lie on that curve (appendix B). For the purpose of this appendix, we have to demonstrate that, for the linear combination, the slope SV of the local invasion boundary is intermediate between the slopes SV_p and SV_Φ that result from the two extreme scenarios.

Assume that seed production is a linear combination of plant biomass and primary production,

$$F_i = \beta P_i^* + (1 - \beta)\Phi_i^*$$

Then, the slope of the local invasion boundary is

$$SV = \left[-\frac{\partial F_m}{\partial c_m} / \frac{\partial F_m}{\partial u_m} \right]_{c_m=c_r, u_m=u_r}$$

$$= \left[\frac{\beta \left(-\frac{\partial P_m^*}{\partial c_m} \right) + (1 - \beta) \left(-\frac{\partial \Phi_m^*}{\partial c_m} \right)}{\beta \frac{\partial P_m^*}{\partial u_m} + (1 - \beta) \frac{\partial \Phi_m^*}{\partial u_m}} \right]_{c_m=c_r, u_m=u_r}$$

In comparison, the slopes of the local invasion boundaries for the extreme cases where seed production is proportional to plant biomass and to primary production are

$$SV_p = \left[-\frac{\partial P_m^*}{\partial c_m} / \frac{\partial P_m^*}{\partial u_m} \right]_{c_m=c_r, u_m=u_r}$$

and

$$SV_\Phi = \left[-\frac{\partial \Phi_m^*}{\partial c_m} / \frac{\partial \Phi_m^*}{\partial u_m} \right]_{c_m=c_r, u_m=u_r}$$

respectively. The biomass and primary production of a mutant decrease when the consumption rate increases and increase when the uptake rate increases. Therefore, the derivatives with respect to the consumption rate, c_m , are negative while the derivatives with respect to the uptake rate, u_m , are positive. As a consequence, it can be shown that both $SV_p - SV$ and $SV - SV_\Phi$ have the same sign as $SV_p - SV_\Phi$.

Further calculations show that

$$SV_p - SV_\Phi = \frac{u(v_p d_p + c)[uI - l(d_p + c)]}{(l + k)(v_p d_p + v_h c)(d_p + c)^2}$$

which is positive under feasible biological conditions: a seed production that is proportional to biomass selects for higher defense levels than does a seed production that is proportional to primary production. This results from the

fact that consumption has a greater negative impact on plant biomass than on primary production.

In summary, the slopes of the invasion boundaries in the different cases can be ranked as follows:

$$SV_p > SV > SV_\Phi.$$

The slope of the local invasion boundary V in the linear combination scenario is therefore intermediate between the slopes for the two extreme scenarios. Consequently,

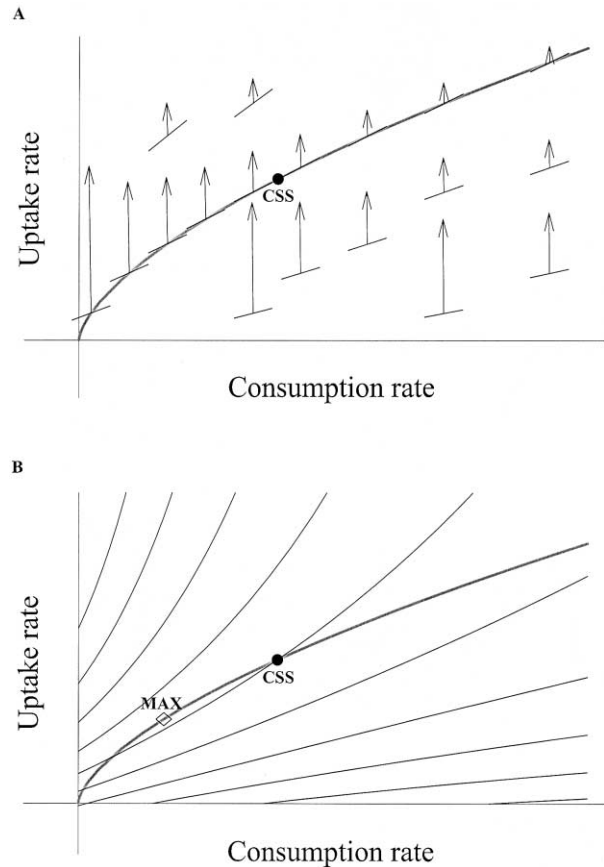


Figure B1: A, Local invasion boundaries and direction of selection (arrows) in the plane of all possible plant strategies (c, u). Each short line indicates the local boundary between invading (above) and noninvading strategies (below) for a resident strategy situated at the midpoint of the line. The continuously stable strategy (black dot) on the trade-off curve (solid line) is located where the invasion boundary is tangential to the trade-off curve. B, Isolines of biomass in the plane of all possible plant strategies (c, u). Biomass is zero for the bottom-right curve and increases toward the upper left. Biomass is maximized along the trade-off curve where the isolines of biomass and the trade-off curve are tangential (open diamond). The corresponding CSS is shown for comparison (black dot). Parameters: $l = 28.11 \text{ kgN} \times \text{ha}^{-1} \times \text{yr}^{-1}$; $I = 1.80 \text{ yr}^{-1}$; $k = 10.79 \text{ yr}^{-1}$; $d_p = 2.15 \text{ yr}^{-1}$; $v_p = 0.26$; $v_h = 0.72$. Trade-off function: $c_{\min} = 2.54 \text{ yr}^{-1}$; $c_{\max} = 3.20 \text{ yr}^{-1}$; $u_i = 0.17 + 0.17 (c_i - c_{\min})^{0.63} \text{ ha} \times \text{kgN}^{-1} \times \text{yr}^{-1}$.

along a trade-off curve, the evolutionary outcome for the linear combination scenario will be intermediate between the evolutionary outcomes obtained in the two extreme scenarios.

Figure A1 shows that both ecological and evolutionary mutualisms are possible for cases that are intermediate between the two extreme scenarios of seed production. Conditions for mutualism become increasingly stringent when plant production is more determined by plant biomass than by primary production.

APPENDIX B

Locating CSSs and Maximizing Strategies along the Trade-off Curve

In a population consisting of one resident strategy, with consumption rate and nutrient uptake rate (c_r, u_r), we analyze which other strategies are able to invade, when rare, into the resident population. In the plane (c, u) of all consumption and uptake rate, for each resident strategy, we determine an invasion boundary, separating strategies that can invade from those that cannot. With F_m denoting the seed production of a rare mutant with parameters (c_m, u_m) when rare in the resident population, the slope of the invasion boundary is given by

$$SV = \left[-\frac{\partial F_m}{\partial c_m} / \frac{\partial F_m}{\partial u_m} \right]_{c_m=c_r, u_r=u_r}$$

Evolutionary outcomes can be determined graphically by plotting the trade-off curve together with the local invasion boundaries, as determined by their slope. Figure B1A shows the invasion boundaries (straight line segments) at some points (c, u) of the set of strategies: each boundary separates the strategies that are capable and incapable of invading the resident strategy (c_r, u_r) at the midpoint of the segment. The corresponding arrow shows the strength and direction of selection from the considered resident strategy. A CSS is located at a point along the trade-off curve where the invasion boundary is tangential to the trade-off curve. This condition is not sufficient for this point to be a CSS; more methodological details can be found elsewhere (de Mazancourt et al. 1998; C. de Mazancourt, M. Loreau, and U. Dieckmann, unpublished manuscript).

Similarly, the strategy maximizing plant biomass can be found by plotting the trade-off curve together with the isolines of equilibrium biomass (fig. B1B). A maximum (or minimum) of plant biomass occurs along the trade-off curve where the biomass isolines are tangential to the trade-off curve. Analogously, the maximum of primary

production occurs at the point where the trade-off curve is tangential to an isoline of primary production.

Comparing the slopes of the invasion boundaries with the isolines of biomass and primary production (fig. B1) therefore allows us to find the relative positions of the strategies that maximize biomass or primary production (MAX_p and MAX_q) and of the evolutionary outcomes that result from plant adaptation under the two scenarios of plant seed production (CSS_p and CSS_q).

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