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Herbivory Promotes Plant Production and Reproduction in Nutrient-Poor Conditions: Effects of Plant Adaptive Phenology

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ABSTRACT: Many studies have demonstrated positive effects of herbivory on plant performance, and these encompass two categories of effects: enhancement of primary production and enhancement of reproductive success. These positive responses of plants to herbivory have been called "grazing optimization." One possible mechanism of these paradoxical phenomena is the nutrient cycling promoted by herbivory. This article models the nutrient cycling hypothesis and analyzes the evolution of plant production and reproduction enhanced by herbivores, using dynamic optimization of plant phenology. Especially when there is nutrient competition among plant individuals or nutrient transportation by herbivores, we can apply the concept of evolutionary stability for the dynamic optimization. Two types of plant responses, long-term and short-term, are examined. Long-term response is an adaptive response for a given level of herbivory pressure, while short-term response is a nonadaptive one to various levels of herbivory, different from the level to which the plant is adapted. The analysis shows that both long-term and short-term grazing optimizations in primary production can occur under poor nutrient conditions and high nutrient recycling rates. However, grazing optimization in reproduction occurs under the same conditions but requires further conditions. In particular, long-term reproductive grazing optimization occurs only when nutrient competition exists among plant individuals. Accordingly, the present analysis revealed the following points concerning grazing optimization: poor nutrient condition is necessary, nutrient competition between plant individuals can promote optimization, and the native condition of the plant is important in the short-term response.

Keywords: plant phenology, grazing optimization, nutrient cycle, model, dynamic optimization.

Many studies have demonstrated positive effects of herbivory on plant performance in primary production (Dyer 1975; Dyer and Bokhari 1976; McNaughton 1976, 1979, 1983, 1985; Owen and Wiegert 1976; Hilbert et al. 1981) and reproductive success (Paige and Whitham 1987; Lennartsson et al. 1997, 1998; Paige 1999). These positive responses of plants to herbivory have been called "grazing optimization" (McNaughton 1976) or "overcompensation" (Paige and Whitham 1987). The former phrase tends to represent a plant's positive responses (often in production) to long-term herbivory disturbance, whereas the latter is likely to refer to responses (often in reproduction) to short-term disturbance. These effects have frequently been discussed as a mutualistic coevolution between plants and herbivores (Järemo et al. 1999; de Mazancourt et al. 2001).

In order to explain how and why grazing optimization occurs, several hypotheses have been proposed, including the following: herbivory promotes nutrient cycling, herbivory increases light intensity reaching more active underlying tissues, and herbivory changes hormonal distribution by removing apical dominance. The explanation of the first hypothesis is not straightforward and requires theoretical analysis. The basic mechanisms of grazing optimization on the nutrient cycling hypothesis have been investigated by several authors (Dyer et al. 1986; DeAngelis 1992; Loreau 1995; de Mazancourt et al. 1998, 2001; de Mazancourt and Loreau 2000*a*, 2000*b*). In addition to these, more complicated models based on real data have also been proposed to simulate grazing optimization (Carpenter and Kitchell 1984; Holland et al. 1992; de Mazancourt et al. 1999). These studies successfully indicated that nutrient cycling can result in grazing optimization. In particular, de Mazancourt and coworkers showed that grazing optimization occurs if nutrient loss is low in the nutrient cycle by herbivores grazing on plants and if a nutrient input into the system is larger than a certain critical level (de Mazancourt et al. 1998, 2001; de Mazancourt and Loreau 2000*a*). Most of these studies focused on the equilibrium state of nutrient dynamics, in which all parameters are fixed, ignoring the evolution of traits in the organisms.

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Only de Mazancourt and Loreau (2000*b*) and de Mazancourt et al. (2001) included an evolutionary aspect in the model, in which they analyzed the resource allocation between growth and defense that could be attained through the evolutionary process.

Models ignoring life-history aspects seem applicable to simple organisms such as plankton, where the fitness of organisms can be measured by biomass. However, if we consider taxonomically higher plants, the model should include more detailed life history of the plants. In order to understand plant responses to herbivory, we should focus on the nutrient consumption pattern of plants, that is, the biomass allocation schedule or phenology. Among the studies that have considered evolution of the schedule of biomass allocation in plants, a mathematical approach that was initially developed by Cohen (1971, 1976) has played an important role. Thereafter, dynamic optimization models have successfully contributed to investigations on the evolution of plant phenology (King and Roughgarden 1982*a*, 1982*b*, 1983; Schaffer 1983; Iwasa and Roughgarden 1984; Iwasa and Cohen 1989; Iwasa 1991; Yamamura and Tsuji 1995; Iwasa et al. 1996; Iwasa and Kubo 1997). These studies have explained the resource allocation patterns between various tissues in a plant, which dynamically change during its life cycle.

In the nutrient cycling hypothesis, primary production depends on both nutrient and herbivory conditions. Those conditions must affect the plant phenology as an evolutionary response or optimal phenotypic plasticity. This article theoretically analyzes a mechanism resulting in grazing optimization with respect to primary production and reproductive success, focusing on the optimal response in plant phenology, by using the dynamic optimization approach. When there is nutrient competition among plant individuals or nutrient transportation by herbivores, we apply the concept of evolutionary stability (Maynard Smith 1982) for dynamic optimization.

In the following analysis, categories of grazing optimization will be clarified. We hereafter refer to the grazing optimization in primary production and reproductive success as "productive grazing optimization" and "reproductive grazing optimization," respectively. We consider that productive and reproductive grazing optimizations are detected when the primary production and the final reproduction, respectively, increase with increasing herbivory pressure. From the evolutionary perspective, two types of response should be distinguished: long-term and short-term responses (Järemo et al. 1999; de Mazancourt et al. 2001). Plants that are exposed to a constant herbivory pressure over a long evolutionary period would be expected to have a phenology that is adapted to the condition, such that their reproductive success is maximized. The long-term viewpoint focuses on evolutionary consequences that would result under various given herbivorous pressures. If the plants have the ability to modify their phenotypes so as to adjust to given conditions during the developmental period (i.e., the optimal phenotypic plasticity), the same concept can also be applied. In contrast to this, performance of a fixed strategy that is adjusted to a certain fixed herbivorous pressure may be examined under varying herbivory pressures. Since this examination is not accompanied by the adaptation of plants, it implies a test of the short-term response. Namely, the short-term viewpoint examines the performance of a certain strategy against varying herbivorous pressures. The long-term response may be observed by comparative studies between plant performances of different habitats or by the study of phenotypic plasticity of plants experiencing different levels of herbivory. The short-term response can be examined by using plants experiencing a constant herbivory, comparing their performance under the natural condition and under a manipulated condition, for example, by experiments using enclosures. We clearly distinguish these two types of response in the following analysis of the model.

Mathematical Model

An annual plant species is considered where individuals reproduce once at the end of the season. An individual plant is separated into two parts, vegetative and reproductive, and the nutrient contents of these parts are represented by V and R, respectively. The initial conditions at the beginning of the season are $V = V_0$ (seed size) and $R = 0$. The amount of nutrients included in the soil around the focal individual is denoted by S, with its initial value being S_0. It is assumed that no further nutrients are supplied into the system after this initial amount. The amounts of nutrients in different components (V, R, and S) change dynamically within the growing season.

The assimilation rate of plants can be considered to depend on both individual photosynthetic ability and nutrient availability. The photosynthetic ability should be an increasing function of the size of the vegetative part. The photosynthetic ability may increase more slowly than the size of vegetative part, because a large vegetative part may be accompanied by more costs of maintenance or lower light intensity due to self-shading. Thus, the photosynthetic ability is assumed to be a convex function of the size of the vegetative part, $\alpha_1 V^{\gamma}$ $(0 < \gamma < 1)$. The photosynthetic products (e.g., glucose and other carbohydrates) are considered to become biomass going to growth (e.g., proteins, lipids, etc.) through consumption of nutrients. Since the nutrients are usually limiting the plant's production, the production rate of biomass will depend on nutrient availability. The transformation rate of the photosynthetic products to biomass is given as $\alpha_2(1 - e^{-\beta S})$, which implies that the rate increases with an improvement of nutrient conditions, S. Consequently, denoting $\alpha = \alpha_1\alpha_2$, the assimilation rate is represented as $g(V, S) = \alpha(1 - e^{-\beta S})V^{\gamma}$. In the present analysis, we measure the biomass by the amount of nutrients involved; therefore, $g(V, S)$ represents the rate of nutrient assimilation. The assimilated products are allocated between the growth of vegetative and reproductive parts at each moment. The allocation schedule is optimized so as to maximize the final size of the reproductive part, $R(T)$, where T represents the end of the season. The resource allocation into the reproductive part at time t is denoted by $x(t)$. In the present study, four models are proposed with different patterns of nutrient dynamics.

Model 1: Herbivores Graze the Vegetative Part Only, with Nutrients Returning to the Grazed Plant

A scheme of this model is illustrated in figure 1. In this model, the vegetative part is grazed at rate h, but the reproductive part is not. A fraction k of the nutrients return to the soil via excrement of the herbivores. According to the assumptions, the dynamics of the nutrient contents of vegetative and reproductive parts of the plant and soil in the patch are, respectively, formulated by the equations

$$\frac{dR}{dt} = x(t)g(V, S), \tag{1a}$$

$$\frac{dV}{dt} = [1 - x(t)]g(V, S) - hV, \tag{1b}$$

$$\frac{dS}{dt} = -g(V, S) + khV, \tag{1c}$$

where $g(V, S) = \alpha(1 - e^{-\beta S})V^{\gamma}$. The individual plant in question chooses $x(t)$ so as to maximize the final size of the reproductive part, $R(T)$. This type of problem can be solved by Pontryagin's maximum principle (Pontryagin et al. 1962). On the basis of the dynamics (1), the Hamiltonian is formulated as

$$H = \frac{dR}{dt} + \lambda_0\frac{dR}{dt} + \lambda_1\frac{dV}{dt} + \lambda_2\frac{dS}{dt}, \tag{2a}$$

where λ_0, λ_1, and λ_2 are auxiliary variables. The dynamics of these variables are denoted by

$$\frac{d\lambda_0}{dt} = -\frac{\partial H}{\partial R}, \tag{2b}$$

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial V}, \tag{2c}$$

$$\frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial S}, \tag{2d}$$

where the final values $\lambda_0(T)$, $\lambda_1(T)$, and $\lambda_2(T)$ are 0. Since equation (2b) is 0 in the present model, $\lambda_0(t)$ is constant, being 0 for all t. According to the maximum principle, the optimal resource allocation schedule $x^*(t)$ can be derived by choosing $x(t)$ that maximizes the Hamiltonian H at each moment. According to the appendix in the online edition of the *American Naturalist*, the solution at each moment is

$$x^*(t) = \begin{cases} 0 & \text{if } 1 < \lambda_1 \\ 1 & \text{if } 1 > \lambda_1 \end{cases}. \tag{3}$$

This optimal resource allocation strategy is "bang-bang control," which often appears in the optimal solutions obtained by the maximum principle, in which the optimal control is completely switched (never being $0 < x^*(t) < 1$). For a set of given parameter values, the solution is numerically derived by using a computer.

In the numerical analysis, the initial values of variables, $(R_0, V_0, S_0, \lambda_{1,0}, \lambda_{2,0})$, are first given, where $\lambda_{1,0}$ and $\lambda_{2,0}$ are randomly determined. Once variables at time t are given as $(R(t), V(t), S(t), \lambda_1(t), \lambda_2(t))$, the optimal solution of this moment, $x^*(t)$, can be solved from equation (3).

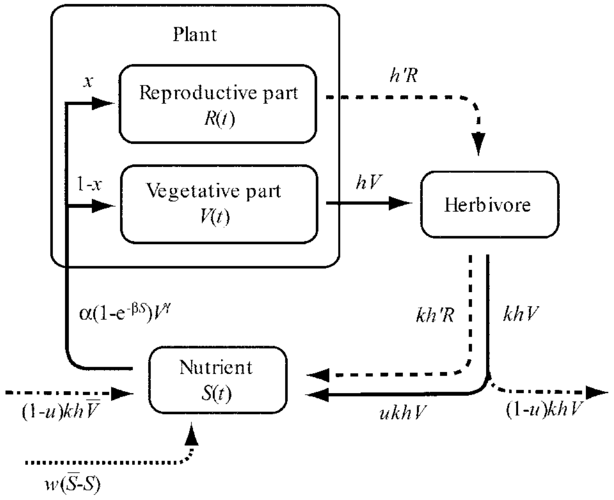

Figure 1: Schemes of the model considered. In model 1, $h' = 0$, $w = 0$, and $u = 1$ (*solid lines*). In model 2, $h' > 0$, $w = 0$, and $u = 1$ (*including dashed lines*). In model 3, $h' = 0$, $w > 0$, and $u = 1$ (*including dotted line*). In model 4, $h' = 0$, $w = 0$, and $0 < u < 1$ (*including dashed-and-dotted lines*).

Using the solution $x^*(t)$, the variable set of the next moment, $(R(t+1), V(t+1), S(t+1), \lambda_1(t+1), \lambda_2(t+1))$, can be determined from equations (1) and (2). By iterations, the variables and solution can be determined from time 0 to T. When the procedure is complete, $\lambda_1(T)$ and $\lambda_2(T)$ are examined. If these values do not equal to 0, the procedure is repeated, changing $\lambda_{1,0}$ and $\lambda_{2,0}$ slightly. A series of procedures are repeated until both $\lambda_1(T)$ and $\lambda_2(T)$ coincide with 0. When $\lambda_1(T)$ and $\lambda_2(T)$ become 0, the derived variables $(R(t), V(t), S(t))$ and $x^*(t)$ represent the optimal growth and allocation schedule, respectively.

Model 2: Herbivores Also Graze on the Reproductive Part, with Nutrients Returning to the Grazed Plant

Herbivores are assumed to graze the reproductive part as well as the vegetative part. In this case, equation (1) can be rewritten as

$$\frac{dR}{dt} = x(t)g(V, S) - h'R, \tag{4a}$$

$$\frac{dV}{dt} = [1 - x(t)]g(V, S) - hV, \tag{4b}$$

$$\frac{dS}{dt} = -g(V, S) + k(h'R + hV), \tag{4c}$$

where h' represents a herbivory rate on the reproductive part. Equation (4) is obtained by adding $-h'R$ and $kh'R$ to equations (1a) and (1c), respectively. The optimal resource allocation schedule can be obtained by the same method as that in the previous model.

Model 3: Nutrient Is Transported between Patches by Diffusion

In the above models, a plant is assumed to monopolize nutrients within its own patch, without any nutrient transport among patches. However, the nutrients may diffuse between patches along a density gradient. In such a case, an individual that consumes more nutrients than others can receive more nutrients from other patches, resulting in nutrient competition among plant individuals. Since the plants interact with each other via nutrient transportation, the growth strategy of a certain individual is affected by the strategies of others. Therefore, the "game" that occurs among individuals in the population should be considered. This type of problem can be solved by considering the dynamic evolutionarily stable strategy (Wakano et al. 2002). In this section, the nutrient diffusion between patches is added to model 1.

In order to determine the evolutionarily stable phenology, $\bar{x}^*(t)$, we search for a solution that satisfies the following condition. Suppose that a rare mutant phenology $x(t)$ occurs in a population where all members adopt a homogeneous phenology schedule $\bar{x}(t)$. In the population, the phenology that maximizes the fitness of the mutant is defined by $x^*(t)$. If $x^*(t)$ coincides with wild-type phenology $\bar{x}(t)$, it is an evolutionarily stable phenology, $\bar{x}^*(t)$. This condition coincides exactly with that of an evolutionarily stable state (Maynard Smith 1982). In the analysis, the dynamics of both wild-type and focal mutant have to be formulated.

First, we consider the nutrient dynamics of a rare mutant in the population that is otherwise occupied by a homogeneous strategy. Consider a population in which all members are adopting the evolutionarily stable resource allocation schedule, $\bar{x}^*(t)$, with variables at each moment being $\overline{R}(t)$, $\overline{V}(t)$, and $\overline{S}(t)$. In the population, a mutant adopting the resource allocation strategy $x(t)$ is introduced, whose variables at each moment are represented by $R(t)$, $V(t)$, and $S(t)$. The growth dynamics of the mutant are formulated by

$$\frac{dR}{dt} = x(t)g(V, S), \tag{5a}$$

$$\frac{dV}{dt} = [1 - x(t)]g(V, S) - hV, \tag{5b}$$

$$\frac{dS}{dt} = -g(V, S) + khV + w(\overline{S} - S), \tag{5c}$$

where w represents intensity of nutrient diffusion between patches. The optimal allocation schedule of the mutant $x^*(t)$ can be derived by maximizing the Hamiltonian,

$$H = \frac{dR}{dt} + \lambda_0\frac{dV}{dt} + \lambda_1\frac{dV}{dt} + \lambda_2\frac{dS}{dt}, \tag{6a}$$

at each moment with the dynamics of the auxiliary variables

$$\frac{d\lambda_0}{dt} = -\frac{\partial H}{\partial R}, \tag{6b}$$

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial V}, \tag{6c}$$

$$\frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial S}. \tag{6d}$$

Next, we consider the nutrient dynamics of the wild type. If the optimal resource allocation schedule $\bar{x}^*(t)$ is the evolutionarily stable strategy, the optimal schedule for the mutant $x^*(t)$ must coincide with $\bar{x}^*(t)$, for which the dy-

Table 1: Definitions of variables and parameters

Character	Description
State variables:	
$R(t)$	Reproductive part size
$V(t)$	Vegetative part size
$S(t)$	Amount of nutrients in the soil
$\lambda_0(t)$	Auxiliary variable for $R(t)$
$\lambda_1(t)$	Auxiliary variable for $V(t)$
$\lambda_2(t)$	Auxiliary variable for $S(t)$
Control variable:	
$x(t)$	Allocation strategy between vegetative and reproductive growth
Parameters:	
h'	Herbivory rate on reproductive part
h	Herbivory rate on vegetative part
k	Nutrient recycling rate
α	Exchange coefficient of assimilation rate
β	Dependence of assimilation rate on nutrients in the soil
γ	Dependence of assimilation rate on vegetative part size
w	Nutrient diffusion rate between patches
u	Fraction of nutrients transported to other patch by herbivores

namics of $R(t)$, $V(t)$, and $S(t)$ correspond to those of $\bar{R}(t)$, $\bar{V}(t)$, and $\bar{S}(t)$, respectively. Therefore, $x^*(t)$ must also satisfy

$$\frac{d\bar{R}}{dt} = x^*(t)g(\bar{V}, \bar{S}), \tag{7a}$$

$$\frac{d\bar{V}}{dt} = [1 - x^*(t)]g(\bar{V}, \bar{S}) - h\bar{V}, \tag{7b}$$

$$\frac{d\bar{S}}{dt} = -g(\bar{V}, \bar{S}) + kh\bar{V}. \tag{7c}$$

Setting $V = \bar{V}$ and $S = \bar{S}$ in equations (6b) and (6c), together with the above equations, we can derive the optimal resource allocation schedule by choosing $\lambda_{1,0}$ and $\lambda_{2,0}$ that satisfy both $\lambda_1(T)$ and $\lambda_2(T)$ being 0. By solving this problem, we obtain the evolutionarily stable phenology that does not allow invasions of different phenologies.

Model 4: Nutrient Is Transported between Patches via the Herbivore's Egestion

In the above models, herbivores are assumed to be restricted to an individual plant without long-range movement (e.g., insect larvae). When herbivores are relatively large (e.g., herbivorous mammals), they graze widely. In such a case, nutrients ingested at one patch will be egested in other patches. This factor may affect the optimal strategy of a plant because nutrients transported from other patches are completely out of control of the relevant plant individual. In this section, modifying model 1, it is assumed that egested nutrient khV returns to the focal and different patches with fractions u and $1 - u$, respectively. In this case, the game among individuals in the population should be considered, as in model 3. Consider a population in which all members are adopting the evolutionarily stable resource allocation schedule, $\bar{x}^*(t)$, with the variables at each moment being $\bar{R}(t)$, $\bar{V}(t)$, and $\bar{S}(t)$. In the population, a mutant adopting the resource allocation strategy $x(t)$ is introduced, whose variables at each moment are represented by $R(t)$, $V(t)$, and $S(t)$. The growth dynamics of the mutant are formulated by

$$\frac{dR}{dt} = x(t)g(V, S), \tag{8a}$$

$$\frac{dV}{dt} = [1 - x(t)]g(V, S) - hV, \tag{8b}$$

$$\frac{dS}{dt} = -g(V, S) + ukhV + (1 - u)kh\bar{V}. \tag{8c}$$

The optimal schedule of the mutant $x^*(t)$ can be derived by the same procedure as in model 3.

Results

The models were solved numerically. The relevant variables and parameters are summarized in table 1. According to the solution, we can calculate the total annual primary production under various herbivorous pressures. Initially, we focus on the results of model 1. According to the analysis, the optimal resource allocation strategy generally became bang-bang control, which often appears in optimal solutions obtained by the maximum principle, in which the optimal control is completely switched at a certain time. In solutions of the models, all resources are spent on the vegetative part of growth before a critical time τ, while they are spent on only the reproductive part after τ. Therefore, the optimal strategy of the plant can be characterized by the optimal switching time τ. Figure 2 illustrates the long-term consequence of model 1, varying the initial nutrient conditions for each column, where other parameter values were set as $\alpha = 0.06$, $\beta = 0.1$, $\gamma = 0.8$, $k = 1$, $V_0 = 0.2$, $R_0 = 0$, and $T = 200$. The upper row of the figure shows the optimal switching time τ for given herbivory rates. The optimal switching time of allocation tends to increase with increasing herbivorous pressure, although the tendency is not remarkable when the initial nutrient level is high. The lower row of the figure illustrates the total annual primary production. The primary production can be separated into three components: a final reproductive part size $R(T)$, a final vegetative part size $V(T)$, and a total loss of plant body that is grazed by herbivores during the season. A total primary production increase with increasing herbivory pressure implies the productive grazing optimization. We can see that long-term productive optimization is observed when the nutrient conditions are poor (fig. 2*b*, 2*c*). However, a final increase in the size of the reproductive part $R(T)$ with increasing herbivory pressure implies the reproductive grazing optimization. In figure 2, long-term reproductive optimization does not appear for any nutrient condition. Figure 3 illustrates short-term consequences of model 1. The upper row of the figure shows performance of a strategy that adapted for the condition without herbivores under varying herbivorous pressures, while the lower row indicates performance of a strategy that adapted for a 0.005 herbivory rate. In figure 3, both short-term productive and reproductive optimizations are observed when the plant phenology is adjusted for a degree of herbivorous pressure under poor nutrient conditions.

Both long-term and short-term productive grazing optimizations depend on parameter values. We examined the parameter dependence by computer simulation. When α became larger, there was a shortage of nutrients in the soil because of a high absorption rate of the plant, resulting in both long-term and short-term productive optimization even under richer initial nutrient conditions. An increment of the β value also caused a high nutrient absorption rate, although it did not notably expand the nutrient conditions under which grazing optimization occurs. However, a reduction of β resulted in a disappearance of optimization because of relief of the nutrient shortage. A high γ value promoted growth of the plant by which its photosynthetic ability was improved, resulting in a high consumption of nutrients. Therefore, it tended to cause a shortage of nutrients by which both long-term and short-term productive grazing optimizations arose even under richer initial nutrient conditions. The results also depended on the parameter k, a fraction of the grazed nutrients returning to the soil through herbivore excretion. As k became smaller, both long-term and short-term grazing optimizations were likely to disappear, implying that a reduction of nutrient cycling efficiency suppresses the productive optimization. Especially when the grazed nutrients do not return to plants, the productive grazing optimization was not observed. In such cases, short-term reproductive grazing optimization also tended to disappear, although it could weakly remain under intermediately poor nutrient conditions when the plant adapted to some degree of herbivorous pressure.

Next, model 2 was analyzed, where the reproductive part is also grazed by herbivores. The results are shown in figures 4 and 5, where h' was set to h. In this case, the quantity grazed by herbivores was naturally greater than that in model 1 under the same conditions. According to figure 4, the optimal switching time τ tended to shift to a later time than model 1. In model 1, it is advantageous for plants to allocate more resource to the reproductive part because it is not grazed. Since such an advantage does not exist in model 2, plants prolong the vegetative part growth. In spite of the delay in switching, the qualitative characteristics were similar between the models. The long-term productive grazing optimization occurred under poor nutrient conditions (fig. 4*b*, 4*c*). Both short-term productive and reproductive optimizations were likely to arise when the plant phenology was adjusted for some degree of herbivorous pressure under poor nutrient conditions (fig. 5*b*, 5*c*). However, short-term reproductive optimizations also occur under rich nutrient condition (fig. 5*a*). In addition to this, a weak tendency for short-term productive optimization was also observed when the plant phenology was adjusted for the condition without herbivory under poor nutrient conditions (fig. 5*c*). As the nutrient conditions became poorer, this tendency initially remained but finally disappeared.

Model 3 was also analyzed, where plants compete with each other for nutrients diffusing among patches. The results are shown in figures 6 and 7, where w was set to 0.05. According to figure 6, the nutrient diffusion tends to result in an incremental change of the optimal allocation switching time τ under poor nutrient conditions. Since consumption of nutrient enhances a nutritional inflow from other patches, which increases nutrient availability, plants prolong vegetative growth so as to consume more nutrients. According to such a game among members of the population, the prolonged vegetative growth becomes evolutionarily stable. Figure 6 shows that long-term reproductive grazing optimization weakly occurs under poor

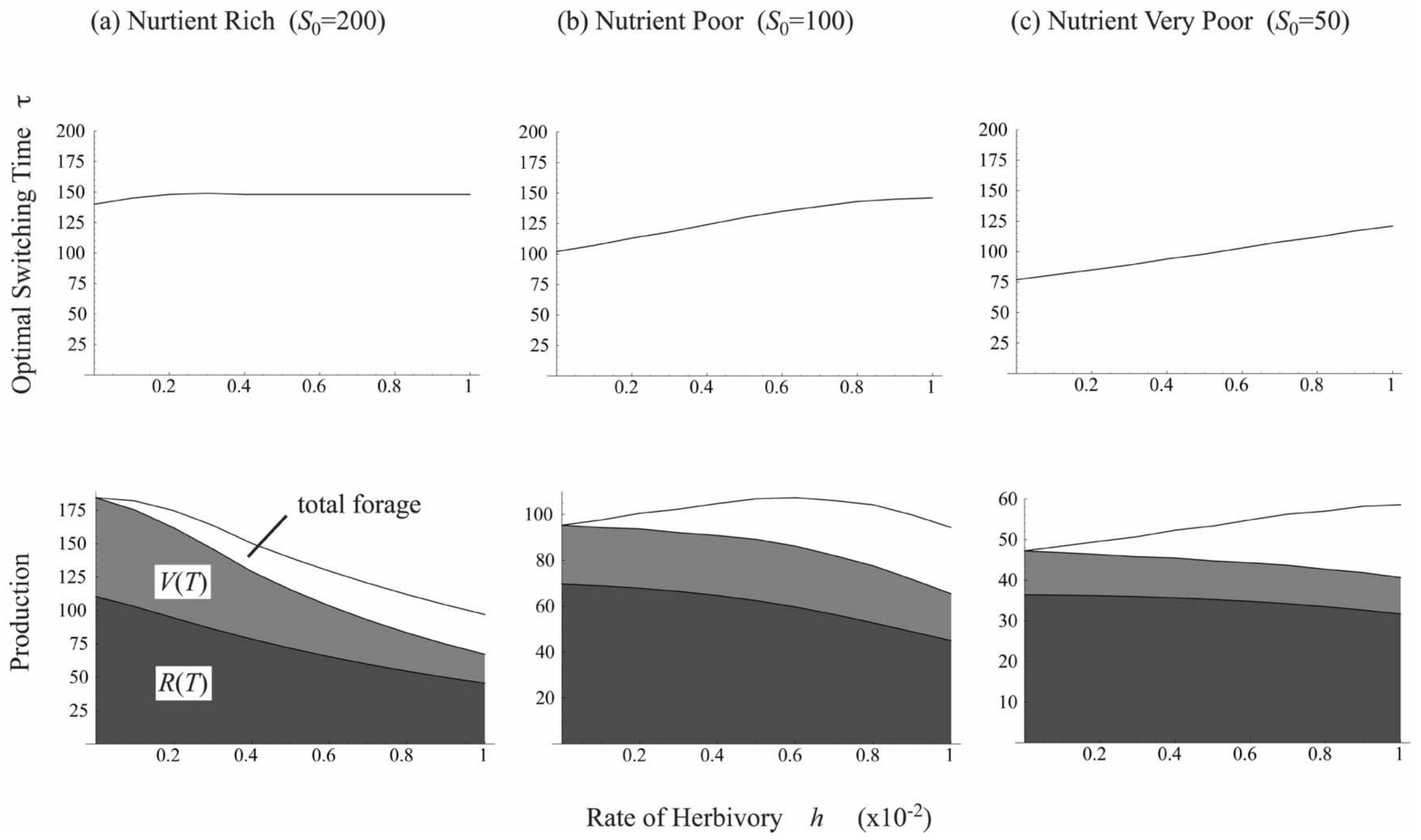

Figure 2: Long-term responses of plants in model 1, varying nutrient conditions for each column. The upper row indicates the optimal switching time τ, and the lower row illustrates the total annual primary production, against herbivory rate. The primary production can be separated into a final reproductive part size $R(T)$, a final vegetative part size $V(T)$, and a total loss of plant body that is grazed by herbivores during the season. Parameters and conditions are $\alpha = 0.06$, $\beta = 0.1$, $\gamma = 0.8$, $k = 1$, $V_0 = 0.2$, $R_0 = 0$, and $T = 200$.

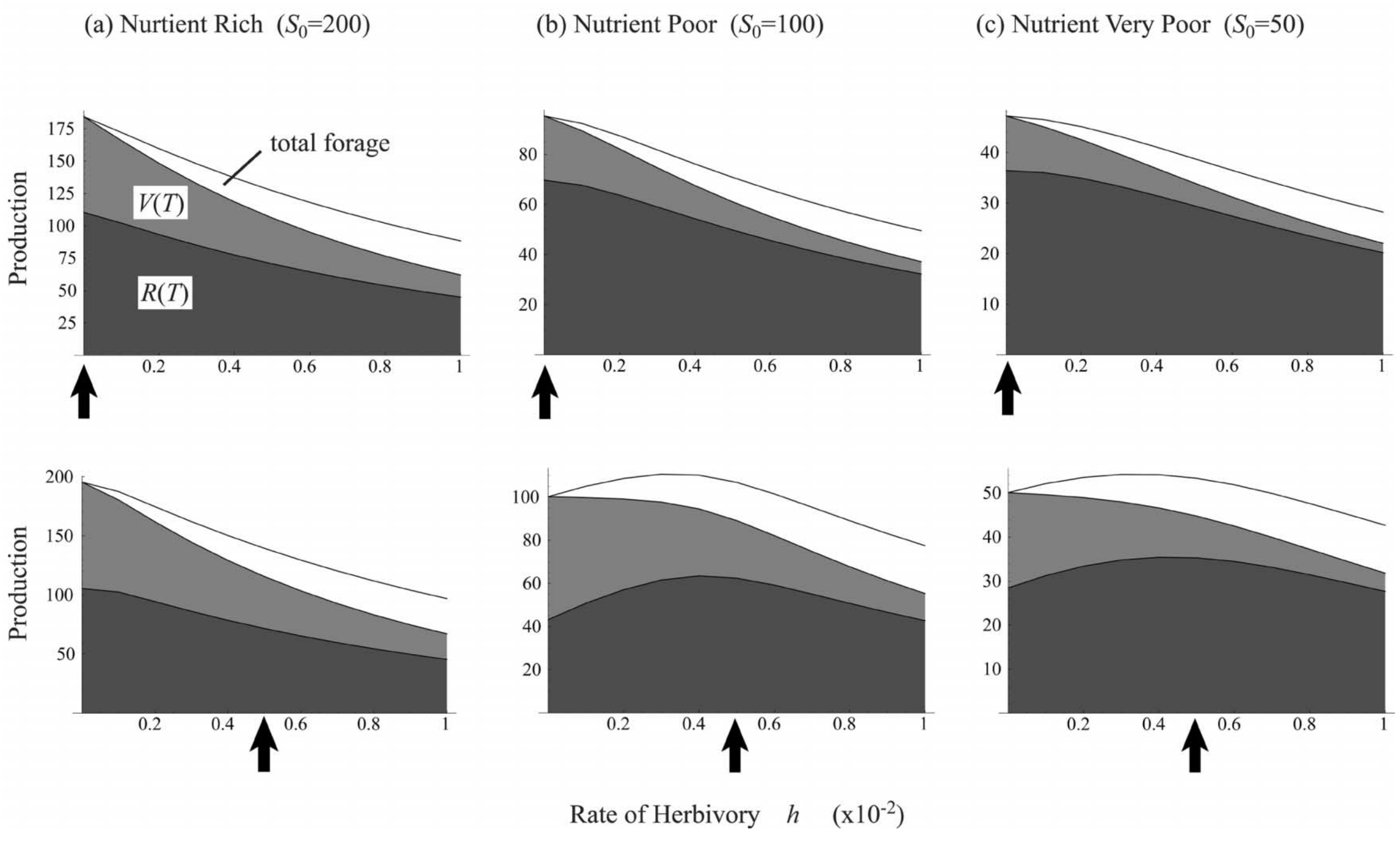

Figure 3: Short-term responses of plants in model 1, varying nutrient conditions for each column. The upper row indicates performance of the strategy that is adjusted in the absence of herbivore, and the lower row illustrates that adjusted for 0.005 herbivory rate, against herbivory rate. Parameter values and conditions are identical to those of figure 2.

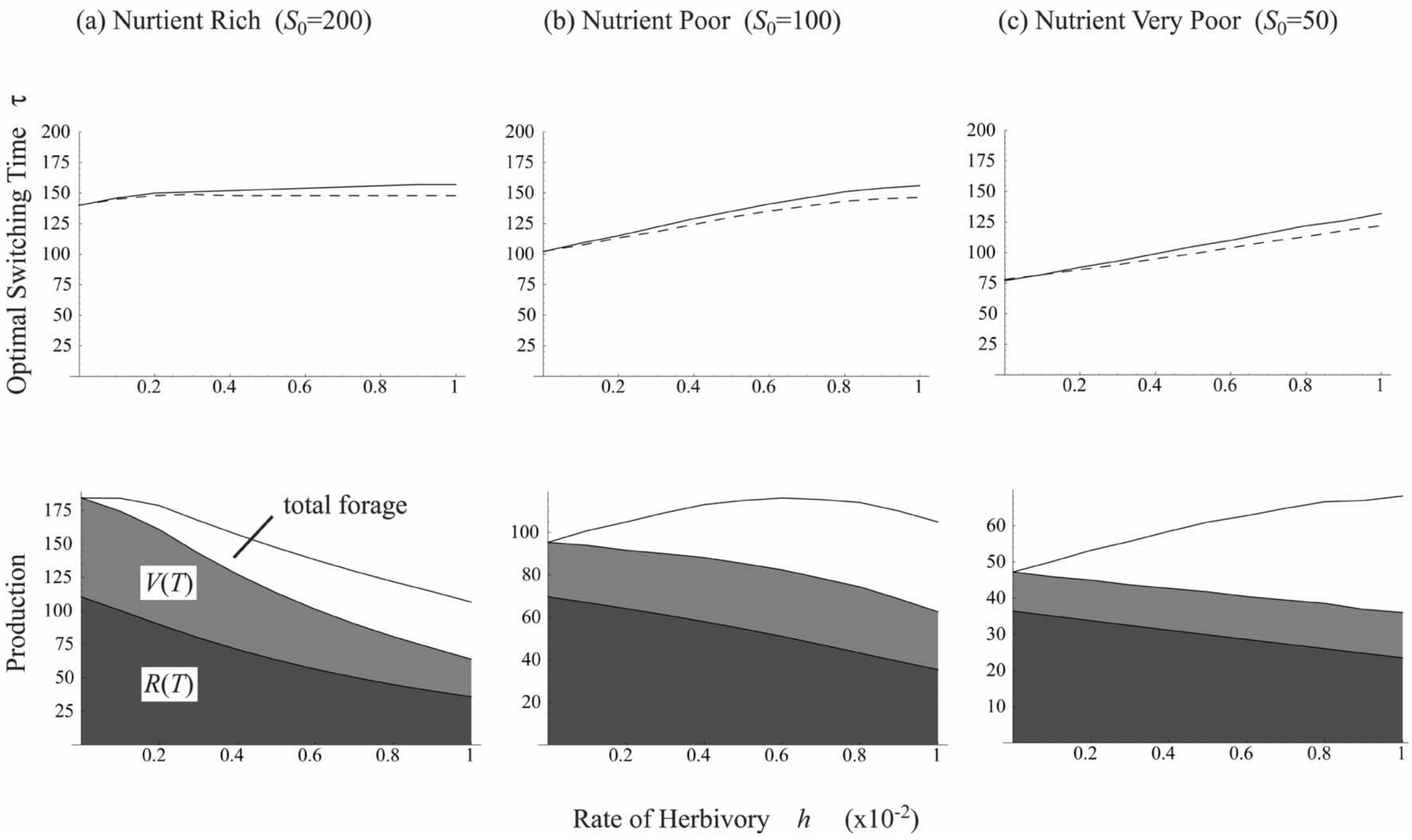

Figure 4: Long-term responses of plants in model 2, varying nutrient conditions for each column. In the upper row, solid lines indicate the optimal switching time τ, with the dashed line being that of model 1. The lower row illustrates the total annual primary production, against herbivory rate. Parameters and conditions are identical to those of figure 2.

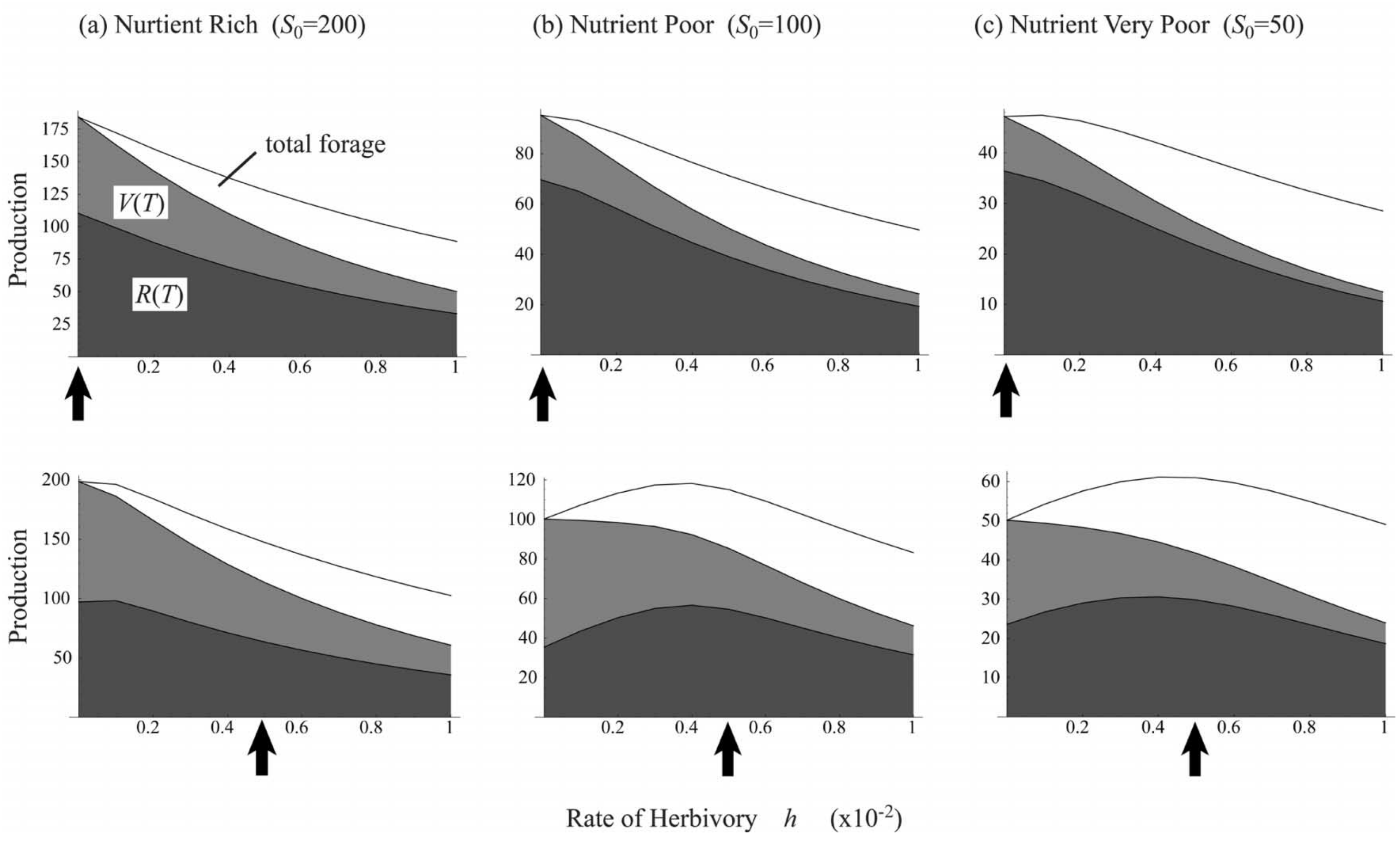

Figure 5: Short-term responses of plants in model 2, varying nutrient conditions for each column. The upper row indicates performance of the strategy that is adjusted in the absence of herbivore, and the lower row illustrates that adjusted for 0.005 herbivory rate, against herbivory rate. Parameter values and conditions are identical to those of figure 2.

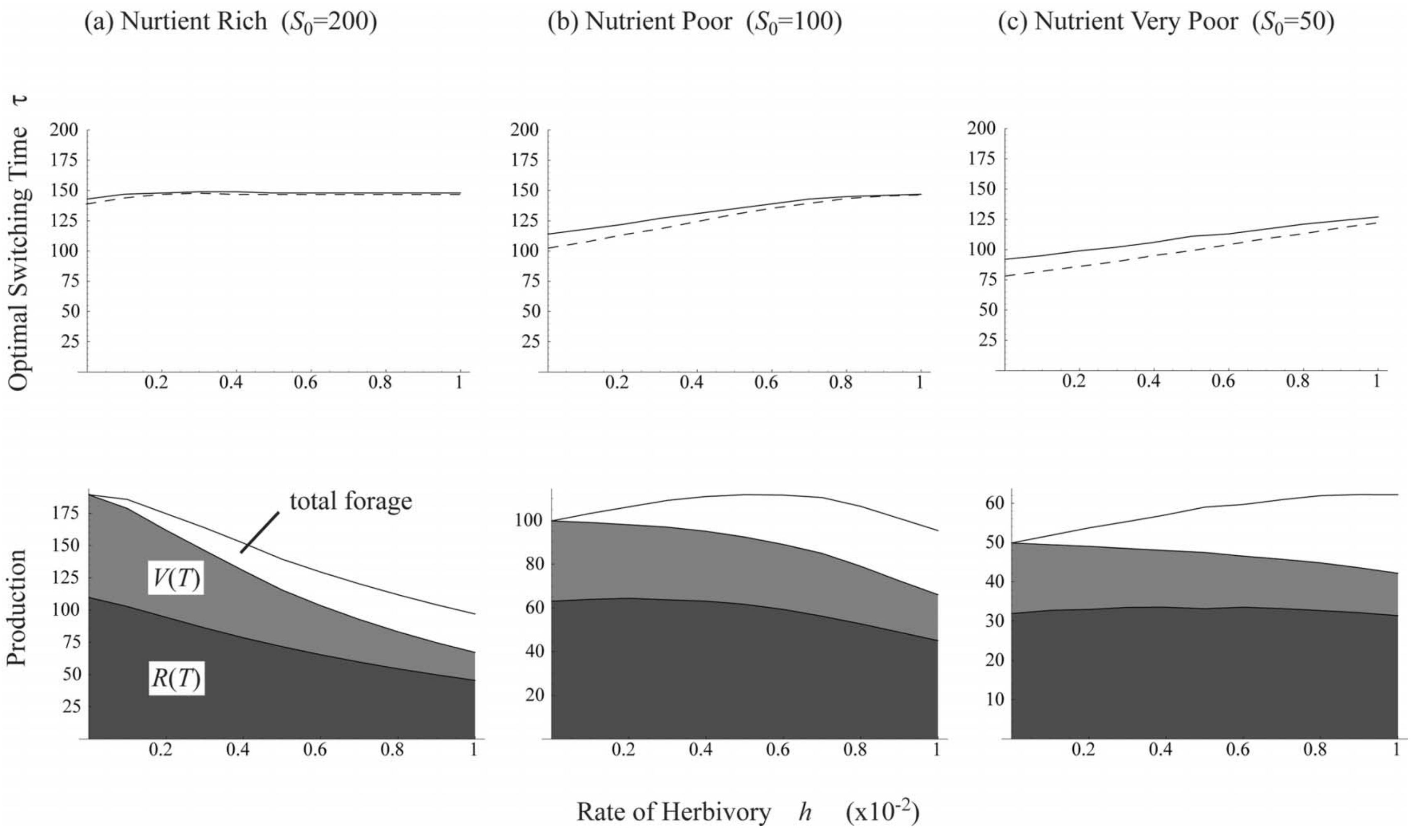

Figure 6: Long-term responses of plants in model 3, varying nutrient conditions for each column. In the upper row, solid lines indicate the optimal switching time τ, with the dashed line being that of model 1. The lower row illustrates the total annual primary production, against herbivory rate. The intensity of nutrient diffusion w is set at 0.05, with other parameters and conditions being identical to those of figure 2.

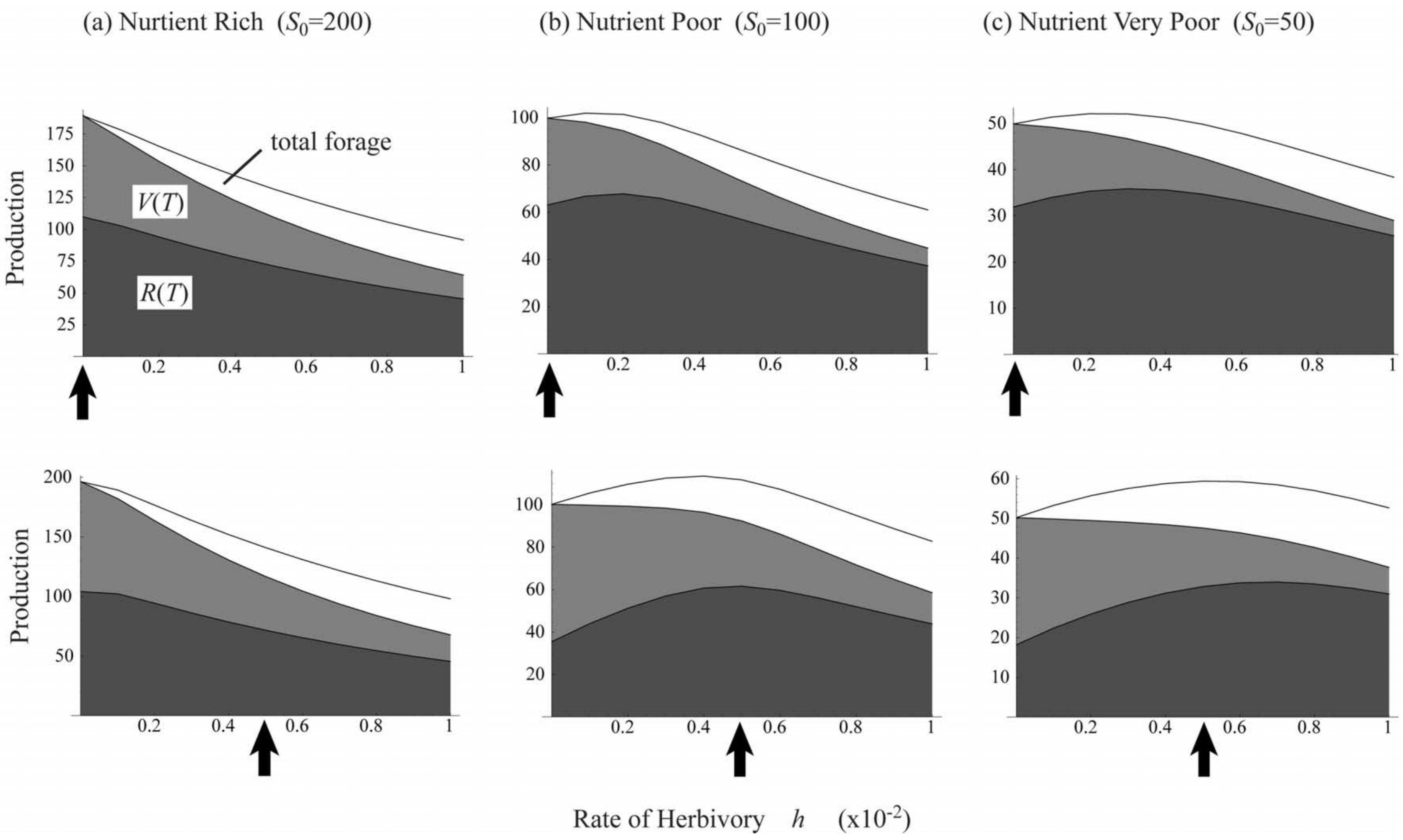

Figure 7: Short-term responses of plants in model 3, varying nutrient conditions for each column. The upper row indicates performance of the strategy that is adjusted in the absence of herbivory, and the lower row illustrates that adjusted for 0.005 herbivory rate, against herbivory rate. The intensity of nutrient diffusion *w* is set 0.05, and other parameters and conditions are identical to those of figure 2.

nutrient conditions. Figure 7 also indicates that even if plants are adapted to the condition without herbivores, both productive and reproductive short-term grazing optimizations arise under poor nutrient conditions. Accordingly, nutrient diffusion among patches tends to promote grazing optimization. This tendency can be explained as follows. Under severe competition, a plant should prolong vegetative growth so as to accumulate more nutrient from other patches even if herbivory level is low. When it is exposed to more severe herbivory, its phenology is accompanied by an additional benefit resulting from the nutrient cycle. Consequently, both production and reproduction are notably enhanced by temporal herbivory, resulting in the promotion of short-term grazing optimizations.

Finally, nutrient transport between patches was analyzed by model 4 where $0 < u < 1$. In this case, under rich nutrient conditions, the optimal switching time of resource allocation τ did not differ from that in the absence of nutrient transport ($u = 1$). Under poor nutrient conditions, the optimal strategy tended to become slightly earlier than the latter when herbivory pressure was high. This may be adaptive for plants under poor nutrient conditions because the earlier cessation of vegetative growth can suppress the drainage of nutrients from its own to other patches through herbivory on vegetative part. However, since the optimal strategy did not significantly vary, the total production and reproduction did not depend much on the extent of nutrient transport. At least within the parameter range examined, the optimal phenology for a plant under the recycled nutrient completely supplied from other patches ($u = 0$) was almost identical to that of all nutrients cycling within its own patch ($u = 1$).

Through all four models, the optimal allocation switching time τ increases with increasing herbivory pressure h for many cases (figs. 2, 4, 6). However, this tendency is not general. In particular, when neither grazing on the reproductive part nor nutrient cycling exists ($k = 0$ in model 1), an increment of herbivorous pressure on the vegetative part is likely to result in a decrement of the optimal switching time. It is advantageous for plants to reduce the investment on the vegetative part that is damaged by foraging. However, the nutrient cycle results in a prolongation of vegetative growth because the former increases the nutrient availability for plants, especially in nutrient-poor conditions. Consequently, the optimal switching time τ can be influenced both positively and negatively by herbivory. In the examined parameter region, the positive effect of nutrient cycling may be dominant, resulting in the optimal switching time being likely to increase with increasing herbivory.

Discussion

We have analyzed theoretically the phenomenon that herbivory promotes performance of plants, that is, grazing optimization. According to the present analysis, both long-term (adaptive) and short-term (nonadaptive) grazing optimizations in primary production can occur under poor nutrient conditions and high nutrient recycling rates (high k). However, grazing optimization in reproduction occurs under the same conditions but further depends on other factors, that is, the strength of nutrient competition and the herbivory levels that plants have experienced. If nutrient competition does not exist among plant individuals, short-term grazing optimization occurs when plants adapt to some degree of herbivory. If nutrient competition is severe, short-term grazing optimization can occur even when plants are optimized to conditions of no herbivory. However, long-term grazing optimization occurs only when nutrient competition exists among plant individuals. Accordingly, if plants follow adaptive responses for different herbivory levels, they can receive higher fitness advantages at higher herbivory levels only under nutrient-poor and competitive conditions. We will first discuss the mechanisms of short-term grazing optimization and next examine the available data on grazing optimization in light of the results of our models.

Mechanism of Short-Term Grazing Optimization

We consider that there are two mechanisms leading to short-term reproductive optimization. One mechanism works when plants have adapted for a high level of herbivory. Such plants tend to adaptively prolong the period of vegetative growth, expecting the following nutrient recycling by herbivore grazing (see figs. 2, 4). Therefore, even when they are set under a low level of herbivory, they would spend much resource on growth of the vegetative part, resulting in a lack of nutrients for growth of the reproductive part. Consequently, the final size of the reproductive part $R(T)$ decreases when herbivory pressure is lower than that under their native condition. The other mechanism relates to the nutrient competition among plant individuals. Plants that are adapted even to conditions of no herbivory demonstrate short-term reproductive optimization when nutrient competition exists (see fig. 7). According to our analysis, such plants adaptively prolong vegetative growth. This phenology becomes advantageous when plants are exposed to some degree of herbivory because they can effectively consume nutrients enhanced by the nutrient cycle, using the prolonged growth period. In other words, the delayed switch of allocation that is optimized to conditions of no herbivory potentially prepares the plant for effective use of recycled nutrient through herbivory. This mechanism may also result in a tendency toward short-term reproductive optimization in model 2 under rich nutrient condition (see fig. 5*a*).

Implications of the Model

The theoretical results obtained indicate that the evolutionary perspective must be taken into account in order to understand the actual phenomenon of grazing optimization. In empirical studies, grazing optimization has often been examined by enclosure of a habitat, where herbivores are excluded from a certain area. Those studies can be regarded as tests of short-term grazing optimization if plants have adapted to a constant herbivory pressure under their own habitats. Several such studies support our prediction that the short-term response of plants varies, depending on the herbivory levels the plants had originally experienced in their natural habitats. Holland et al. (1992) reported that short-term productive grazing optimization occurred in plant individuals collected from populations with grazers but not from those without grazers. Lennartsson et al. (1997) also reported similar consequences in plant reproductive responses.

The plant response that is consistent with the long-term response results not only from evolutionary adaptation but also from optimal phenotypic plasticity. If grazing pressure varies either temporally or spatially, plants may adapt the optimal phenotypic plasticity in their phenology to herbivory, depending on the cost of the plasticity and reliability of the environmental cue (Moran 1992; Scheiner 1993; DeWitt et al. 1998; Tufto 2000). Indeed, some plant species are known to delay the time of flowering, responding to heavy grazing pressure (Young et al. 1994; Ru and Fortune 1999). These delays of flowering under increasing grazing intensity are consistent with a prediction of the present analysis, which is expected as the long-term response of plants. Accordingly, the observed shifts of plant flowering might be a response based on the optimal phenotypic plasticity, concerning the nutrient cycling. Contrary to the phenotypic plasticity adaptation, the evolutionary adaptation of the plant to a constant herbivory pressure may be difficult to test. In order to detect the adaptation, plant performance should be compared between several habitats, among which herbivory pressures have been different but other conditions have been the same, during the evolutionary period.

Both theoretical and empirical studies have often pointed out that grazing optimization concerns nutrient richness, although the presented model predicted that the grazing optimization occurs under poor nutrient condition. Loreau (1995) theoretically predicted that the total quantity of nutrient in the system must be larger than some threshold value for grazing optimization to occur. Generalizing Loreau's model, de Mazancourt et al. (1998) pointed out that grazing optimization required continuous inputs of nutrient into the system being sufficiently great. Their model considered dynamic changes of biomass of herbivore and decomposer, which are not included in the present model. If the herbivore biomass is relatively constant within a season, or if the former is determined by a factor other than food availability (e.g., survival of winter), the dynamics of herbivore biomass may be negligible. For such cases assumed in the present model, the grazing optimization will be observed under poor nutrient conditions.

Maschinski and Whitham (1989) experimentally showed that additional nutrient supplement resulted in significant overcompensation under less competitive conditions. This at first seems inconsistent with our prediction that grazing optimization occurs under nutrient-poor conditions, being enhanced by nutrient competition. This inconsistency relates to their experimental design. In the study of Maschinski and Whitham, both nutritional and competitive conditions were artificially manipulated so as to measure plant performance under various conditions. Under such an experimental design, the short-term response of plants against those temporal conditions may be measured. However, in our analysis, conditions other than herbivory are assumed to be constant during the evolutionary time scale. Namely, we considered long-term response for nutrient and competitive conditions. Considering these differences, we cannot conclude that the results of Maschinski and Whitham (1989) are inconsistent with our results.

The optimal response of plants affects their reproductive consequences. In the absence of nutrient competition, the reproductive success $R(T)$ always decreases with increasing herbivory (see figs. 2, 4), with long-term reproductive grazing optimization never occurring. However, when nutrient competition is introduced, the long-term reproductive grazing optimization is weakly observed under poor nutrient condition (see fig. 6). Such a relationship whereby herbivory enhances plant reproduction as a consequence of evolution (or phenotypic plasticity) can be regarded as a mutualism (Paige and Whitham 1987; Paige 1999; de Mazancourt et al. 2001). The present results suggest that evolutionary mutualism between plants and herbivores may arise, depending on the condition of nutrient competition among plants.

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