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Relative Growth Rates and the Grazing Optimization Hypothesis

D.W. Hilbert, D.M. Swift, J.K. Detling[1], and M.I. Dyer[2]
Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

Summary. A mathematical analysis of the changes in plant relative growth rates necessary to increase aboveground production following grazing was conducted. The equation derived gives an isoline where production of a grazed and ungrazed plant will be the same. The equation has four variables (mean shoot relative growth rate, change in relative growth rate after grazing, grazing intensity, and recovery time) and may be analyzed graphically in a number of ways.

Under certain conditions, small increases in shoot relative growth rate following grazing will lead to increased aboveground production. Under other conditions, very large increases in relative growth rate after grazing can occur without production being increased over that of ungrazed plants. Plants growing at nearly their maximum potential relative growth rate have little opportunity to respond positively to grazing and potentially can sustain less grazing than plants with growth rates far below maximum. Plants with high relative growth rates at the time of grazing require large increases in growth rate while slow growing plants require only small increases. High grazing intensities are least likely to increase production and high grazing frequencies require greater responses than infrequent grazing events.

Introduction

Although herbivores frequently consume only a small proportion of the net primary production (NPP) in terrestrial ecosystems (Owen and Weigert 1976, Golley 1973, Chew 1974), they may have important effects on ecosystem structure and function. Traditionally, only their negative effects on grazed plants have been considered (Mattson and Addy 1975) but it is becoming evident that herbivory may result in a variety of benefits to individual plants, communities and ecosystems. For example, Chew (1974) suggested that herbivores may act as ecosystem regulators by altering productivity and community structure. Analog simulation models incorporating negative feedback from consumers to producers suggest that consumers can dampen deviations from equilibrium and thus perform a homeostatic function in ecosystems (Lee and Inman 1975). Owen and Wiegert (1976) hypothesized that consumers may even maximize plant fitness by improving uptake and cycling of nutrients, an idea which was recently supported by mathematical modeling (Stenseth 1978).

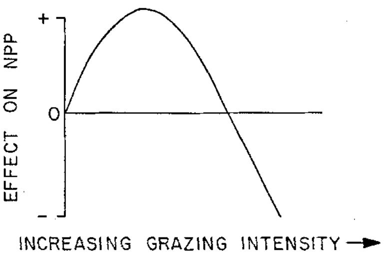

Fig. 1. The grazing optimization hypothesis. Curve shows the change in production due to grazing based on data in Dyer (1975) and McNaughton (1979)

Results of a number of field and laboratory experiments indicate that primary production may be stimulated by grazing under some circumstances (Dyer 1975; McNaughton 1976, 1979; Pearson 1965; Reardon et al. 1972, Smirnov and Tokmakova 1972), and McNaughton (1979) has suggested that aboveground NPP is maximized at some optimum grazing level according to the model shown in Fig. 1. This stimulation of aboveground NPP is referred to as the "grazing optimization hypothesis."

A variety of observed or proposed mechanisms may account for increased primary production following grazing. These include (1) increased photosynthetic rates in tissue remaining or produced after grazing (Hodgkinson et al. 1972; Gifford and Marshall 1973; Detling et al. 1979; Painter and Detling 1981), (2) increased proportion of photosynthate allocated to production of new leaf area (Ryle and Powell 1975; Detling et al. 1979, 1980), (3) increased tillering or lateral bud growth from either removal of apical dominance (Youngner 1972), or opening of the canopy and increasing light penetration (Laude 1972), (4) conservation of soil moisture by reducing transpirational leaf area (McNaughton 1979), and a variety of other indirect mechanisms (McNaughton 1979 and Dyer et al., in press). While these mechanisms are frequently of insufficient magnitude to completely compensate for decreased production resulting from tissue damage or reduced photosynthetic leaf surface area following grazing (Detling et al. 1979, 1980), their existence indicates that plants possess a strong potential for compensatory growth following grazing. Thus, the ability of plants to maximize at least aboveground NPP at light to moderate levels of defoliation by a combination of these mechanisms is a possibility. Using traditional plant growth analysis techniques (Evans 1972), we therefore want to predict the extent to which the plant's relative growth rate must change for a "grazing optimization curve" (Fig. 1) to be produced. To do so, we address the question:

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[1] To whom reprint requests should be addressed

[2] Environmental Science Division, Oak Ridge National Laboratory, Oak Ridge, TN 37830, USA

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How great a change in the relative growth rate of a plant's shoots is necessary, at a given level of grazing, for an increase in aboveground NPP to occur? Answering this question mathematically can clarify the interrelationship between grazing and primary production and suggest the circumstances under which maximization of production is most likely.

Derivation of the Production Isoline

To answer the above question it is necessary to derive mathematical expressions for the production of grazed and ungrazed plants based on their mean relative growth rates. It is then possible to compare these equations and determine a single expression for the stimulus to mean relative growth rate of the grazed plant that is required for increase in production following a grazing event.

Since we desire a completely general statement about this required change, we do not specify any particular model of shoot growth for either the grazed or ungrazed plants. Thus our analysis is applicable under a wide range of conditions. Our only assumption is that biomass is a continuous, monotonically increasing, function of time. We also make no explicit assumption about the time span over which production is considered, although relative growth rates are clearly meaningful only within a single growing season. The analysis simply compares aboveground production of a grazed and ungrazed plant over any given time interval (t_1, t_2) where a single grazing event, of any intensity, occurs at t_1 and the relative growth rate of the grazed plant changes, as a result of shoot removal.

The instantaneous relative growth rate (R) of a plant's shoots is

$$R = \frac{1}{S}\frac{dS}{dt} \tag{1}$$

where S is shoot weight (Blackman 1919). The mean relative growth rate ($\bar{R}$) over a time interval t_1 to t_2 is given by the formula

$$\bar{R} = \frac{\ln S_2 - \ln S_1}{t_2 - t_1} \tag{2}$$

where S_1 is the shoot weight at t_1 and S_2 is the shoot weight at t_2 (Fisher 1921). $\bar{R}$ is the true mean relative growth rate over the time period irrespective of the variations in R that might occur (Fisher 1921; Evans 1972). Thus when the shoot weight of a plant is known at two different times, the mean relative growth rate can be found from Eq. (2) when R is any continuous function.

By rearranging terms in Eq. (2),

$$\ln S_2 = \ln S_1 + \bar{R}(t_2 - t_1). \tag{3}$$

After exponentiating both sides, this becomes

$$S_2 = S_1\, e^{\bar{R}(t_2 - t_1)}. \tag{4}$$

Equation (4) expresses shoot weight at the end of the time period (t_1, t_2) as a function of the initial weight (S_1), the length of the time interval, and mean relative growth rate. Shoot production ($S_2 - S_1$) of ungrazed plants calculated from Eq. (4) is:

$$P = S_1 (e^{\bar{R}(t_2 - t_1)} - 1) \tag{5}$$

where P is production of shoots in the interval (t_1, t_2). While this expression for shoot production has an exponential form, we have not assumed exponential growth of the plant. Rather, Eq. (5) follows directly from the definition of mean relative growth rate [Eq. (2)] which is applicable in situations when $\bar{R}$ is any continuous function. An expression for shoot production of a grazed plant is arrived at similarly. Now, however, the initial shoot weight (S_1) is reduced by some proportion (G) so that at t_1 the shoot weight is $S_1(1-G)$. Also, the mean relative growth rate of the grazed plant ($\bar{R}_g$) may be different than that of the ungrazed plant ($\bar{R}$). Then, similar to Eq. (4),

$$\tilde{S}_2 = S_1 (1-G)\, e^{\bar{R}_g(t_2 - t_1)} \tag{6}$$

where $\tilde{S}_2$ is the shoot weight of the grazed plant at the end of the time interval. Production of the grazed plant ($\tilde{P}$) is then

$$\tilde{P} = S_1 (1-G)(e^{\bar{R}_g(t_2 - t_1)} - 1). \tag{7}$$

We now ask, when will production of the grazed plant be greater than that of the ungrazed plant? Letting $(t_2 - t_1) = \Delta t$ and using Eqs. (5) and (7) $\tilde{P}$ is greater than P when

$$S_1 (1-G)(e^{\bar{R}_g \Delta t} - 1) > S_1 (e^{\bar{R}\Delta t} - 1). \tag{8}$$

By a series of algebraic manipulations, we can now arrive at an expression for the mean relative growth rate of the grazed plant, over the interval Δt, which is required for $\tilde{P}$ to be greater than P. In other words, this is what is required for the optimization hypothesis to be fulfilled. From Eq. (8) we have

$$\bar{R}_g > \frac{\ln \dfrac{e^{\bar{R}\Delta t} - G}{1-G}}{\Delta t}. \tag{9}$$

Expressing (9) as an equality defines the production isoline along which $\tilde{P}$ equals P. We emphasize that this equation does not predict how a grazed plant will respond to grazing, but how it must respond if its production is to equal that of an ungrazed plant. A production isoline is plotted in Fig. 2 by holding Δt and $\bar{R}$ constant in Eq. (9) and plotting ($\bar{R}_g$) as a function of G. The isoline separates the solution space into two

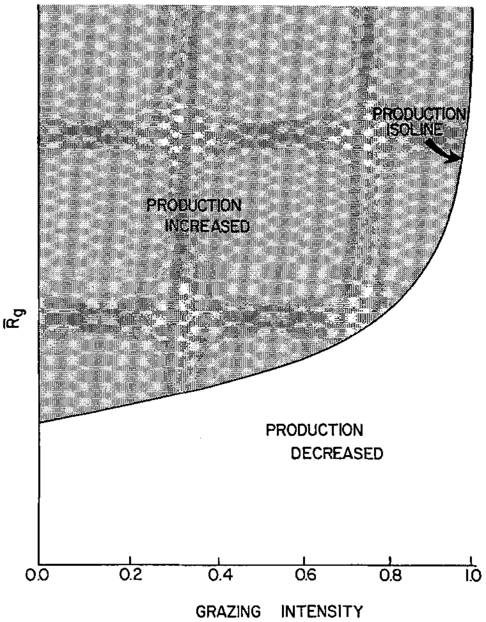

Fig. 2. The production isoline plotted by holding Δt and $\bar{R}$ constant to give $\bar{R}_g$ as a function of G

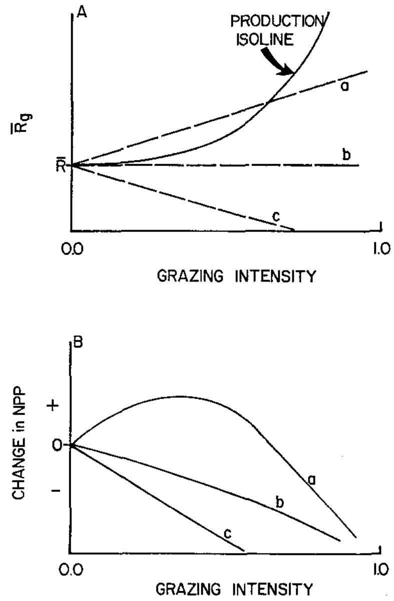

Fig. 3A Three possible responses to grazing (curves **a**, **b**, and **c**) and the production isoline [from Eq. (9)]. Production is increased when the plant response is above the isoline. **B** Changes in aboveground NPP corresponding to curves **a**, **b**, and **c** in Fig. 3A. Change in production is proportional to the distance between the plant response curve and the isoline in Fig. 3A

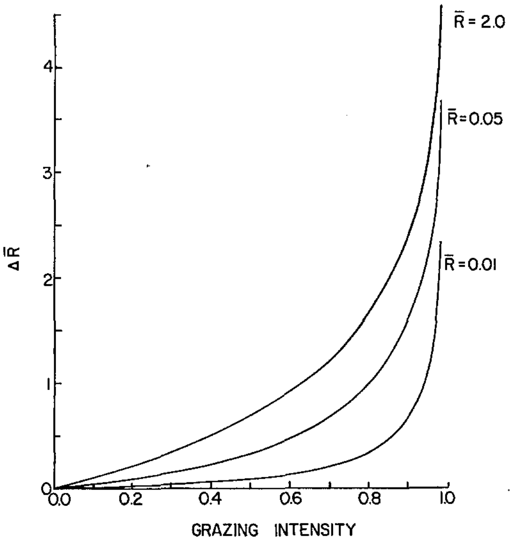

Fig. 4. Relationship between $\bar{R}$ and the production isoline. $\Delta\bar{R}$ is plotted as a function of G with $\Delta t = 10$ and three different values of $\bar{R}$

areas. For a plant grazed at a given level the new growth rate must fall above the isoline for production to increase. A growth rate below the isoline will lead to reduced shoot production.

Analysis

The change in relative growth rate ($\Delta\bar{R} = \bar{R}_g - \bar{R}$) of the grazed plant required to satisfy the condition established by Eq. (9) is variable, and depends upon the mean relative growth rate of the ungrazed plants before grazing ($\bar{R}$), the intensity of grazing (G) and the period over which growth is considered (Δt). Determining how this required change ($\Delta\bar{R}$) varies in response to these variables will help define the conditions under which primary production will most likely be enhanced by grazing.

First, we illustrate how knowledge of a plant's response to grazing, when plotted along with the production isoline, can be used to predict changes in aboveground production. In Fig. 3A we plot a production isoline and three of the many possible relative growth rate responses a plant may make to herbivory. Line (a) represents a plant which responds positively to grazing and increases $\bar{R}$ at all grazing intensities, (b) represents a plant which does not change $\bar{R}$ as a function of G, and (c) represents a plant which decreases $\bar{R}$ in response to grazing. Production is increased when the grazed plant's relative growth rate ($\bar{R}_g$) is above the isoline. Thus, plant (a) increases production at some grazing intensities following herbivory while (b) and (c) both have decreased NPP (Fig. 3B) at all grazing intensities. The change in production at a given level of grazing is a function of the distance between the plant's response curve and the isoline. Where the two cross, production is, of course, equal. Figure 3B gives the expected change in production for the three response curves. Notice that while plant (a) increases $\bar{R}$ for all G, production is still decreased at high grazing intensities. This is a direct result of the very high increases in $\bar{R}$ required at high levels of shoot removal. Line (b) leads to decreasing productivity even though $\bar{R}$ remains constant and line (c) naturally leads to decreased production as well. While these results are somewhat intuitive, we believe that it is often not understood that relative growth rates of plants may be significantly stimulated by grazing without increased production occurring. This type of response has been observed in several experimental defoliation studies (Ryle and Powell 1975; Detling et al. 1979).

The precise shape of the production isoline is a function of the three independent variables: G, $\bar{R}$, and Δt. In effect, the production isoline is actually a surface in four dimensions. To fully describe the effect of these variables, we have simplified the function by holding some of the variables constant.

Figure 4 illustrates the role of $\bar{R}$ at the time of defoliation in determining the required change ($\Delta\bar{R}$). Here, $\Delta\bar{R}$ is plotted as a function of G with Δt constant and three values of $\bar{R}$. This family of curves illustrates that small changes in relative growth rate are required for plants which are growing slowly at the time of grazing while large changes are required for plants with high mean relative growth rates. If small positive changes in $\bar{R}$ are a more probable response to grazing than large ones, then plants growing slowly are more likely to maximize production than those with rapid relative growth rates. This conclusion is strengthened when the plant's growth rate relative to its potential maximum (Grime and Hunt 1975) is considered. In Figure 5 three isolines are plotted, each with a different initial growth rate $\bar{R}$ but with Δt constant. The line labeled $R_{\max}$ represents the maximum relative growth rate of some hypothetical plant species. This line constrains the possible responses of the plant to grazing since, no matter what mechanisms are operating to increase $\bar{R}$ following grazing, $\bar{R}_g$ cannot fall above the $R_{\max}$ line. The intersection of $R_{\max}$ and the isoline gives the maximum grazing intensity beyond which production must decrease, since for grazing intensities beyond this point the required relative growth rate R_g is greater than $R_{\max}$. Plants with growth rates which are low compared to their maximum rate can potentially maximize production at higher optimal grazing intensities than plants with growth rates near their maximum. Thus, Figs. 4

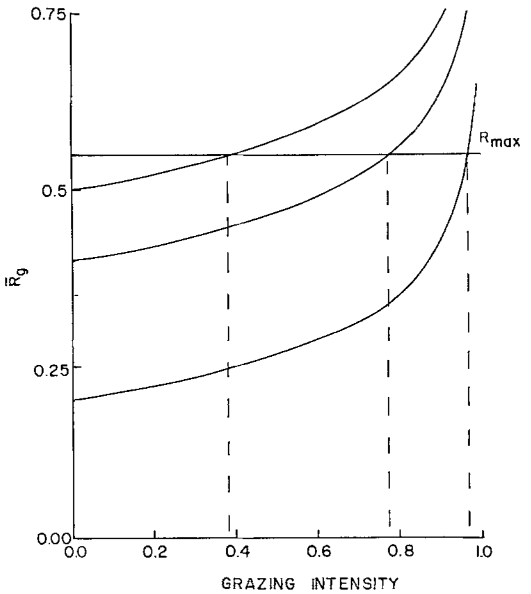

Fig. 5. Three production isolines with three different values of $\bar{R}$, $\Delta t = 10$. $R_{\max}$ is the maximum possible relative growth rate of a hypothetical plant species

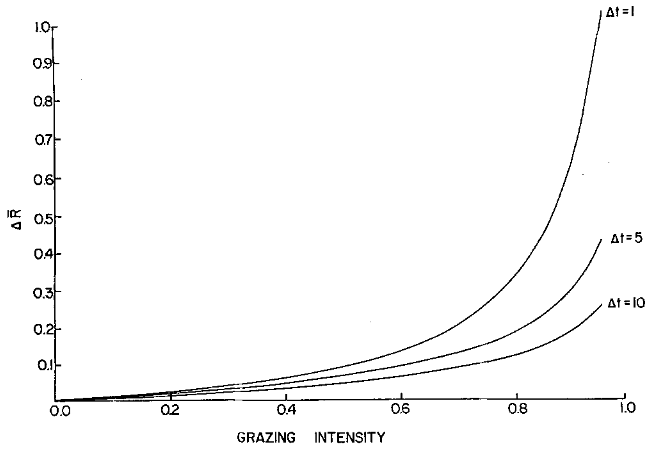

Fig. 6. Effect of the time interval Δt on the production isoline. Three production isolines with $\bar{R} = 0.1$ and three values of Δt

and 5 indicate that the relative growth rate at the time of defoliation (i.e., the growth rate of similar but ungrazed plants) is important in determining the ability of these plants to maximize production following grazing.

The analysis suggests that plants which are stressed in some way, and consequently growing slowly compared to their potential rates, are most likely to increase production following grazing. A study by Hodgkinson (1976) supports this prediction. In this defoliation experiment, irrigated grasses with high $\bar{R}$ decreased production following clipping while the same species increased production when defoliated under water stress which lowered relative growth rates.

In Fig. 6, $\bar{R}$ was held constant and three values of Δt are used to illustrate the effect of time on the production isoline. The increase in relative growth rate necessary for increased production becomes smaller when the plant is given longer to recover from the grazing event. If Δt is considered as a measure of grazing frequency, this suggests that infrequent grazing events are more likely to produce an optimization curve than repeated grazing at short intervals.

This effect of the time over which production is considered has practical importance in the design of defoliation studies as well. Comparing production of defoliated and nondefoliated plants over short periods could overestimate the detrimental effects of clipping on production since very high changes in relative growth rate would be required. Very long time periods, on the other hand, would lead to increased or equal production of defoliated and control plants when only slight stimulation of relative growth rates occur. The mechanisms which can operate to increase $\bar{R}$ following grazing may not, however, be operational for long periods of time. Thus even slightly increased mean relative growth rates, over long periods of time, may be difficult for plants to achieve.

Conclusions

This analysis demonstrates that there is a complex relationship between relative growth rates and production following grazing. In some circumstances, small increases in mean relative growth rates are sufficient to increase production while in other cases, very large changes are required. Thus, the occurance of physiological mechanisms which increase relative growth rates after grazing does not necessarily imply that grazing will increase aboveground production. Conversely, failure to demonstrate increases in production of grazed plants does not negate the possibility that mechanisms are operating to increase growth rates and to minimize losses due to herbivory.

We believe that relative growth rate is a useful measure which integrates a large number of physiological responses to the environment of which grazing is a part and we encourage its use in defoliation studies. Relative growth rates represent production per unit of producing tissue and thus may be an important measure of plant response to grazing.

Grazing modifies the physiology and structure of grazed plants in complex ways and, at the same time, can profoundly affect the interactions between the plant and its abiotic and biotic environment (McNaughton 1979, In press, Youngner 1972). Considering the complexity of these interactions, it appears likely that relative growth rates are always changed by grazing. The type and degree of these responses in relative growth rate determine the effect of herbivory on primary production and hence ecosystem trophic dynamics.

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