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COMPENSATING GROWTH OF GRAZED PLANTS AND ITS RELEVANCE TO THE USE OF RANGELANDS[1]

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Abstract. There are several well-known mechanisms by which grazing can reduce the subsequent growth rate of plants, and several other well-documented mechanisms by which grazing can enhance plant growth rate. The net effect of single or repeated grazing events on the cumulative growth of plants may thus be zero, negative, or positive, depending on availability of leaf area, meristems, stored nutrients, and soil resources, and on the frequency and intensity of defoliation. Plants are preadapted to compensate, up to a certain point, for losses due to grazing, by virtue of their modular structure and development.

Reports of "overcompensation" to grazing, as one extreme of a wide range of responses observed in natural grasslands, need not be treated with special skepticism; neither are they a solid base for a general theory of evolved grass–grazer mutualism. The question of compensatory growth is of relevance to management of Western rangelands for livestock production, but of relatively little relevance to conservation goals. No region-wide answers can be expected. Any drastic change in grazing intensity in either direction requires evaluation by community-specific and long-term research.

Key words: compensatory growth of grazed plants; grazing; herbivory; primary production; range management.

The paper that opens this Forum (Painter and Belsky 1993) addresses two questions, the one scientific, the other practical: Does grazing increase production of plants and why? Should livestock grazing on Western U.S. rangelands be either banned, or intensified? I do not attempt a detailed critique of this paper, nor of previous ones on both sides of the controversy (e.g., Belsky 1986, McNaughton 1986); I try to organize some ideas on these issues.

In the following, "grazing" will be a short term for "removal of shoot parts by grazers, or by any other agents," "growth" will stand for "the net rate of accumulation of shoot biomass," and "production" for "cumulative growth."

MECHANISMS OF NEGATIVE AND POSITIVE EFFECTS OF GRAZING ON GROWTH

There are several mechanisms by which grazing can have immediate negative effects on the subsequent growth rate of a plant (compared with an ungrazed plant in the same conditions), and on its production up to any point in time:

1) Reduction of the photosynthetic leaf area;

2) Removal of active apical meristems that act as sinks for photosynthates and produce new shoot tissues;

3) Loss of nutrients for growth stored in the shoot.

There are also some mechanisms by which grazing can have positive effects on the growth rate of a plant (compared with an ungrazed plant), counteracting these negative effects. Some of these are immediate; others involve a certain delay. In certain circumstances they can conceivably fully compensate or "overcompensate" for the negative effects when eventual production is measured:

1) Increase in light intensity to remaining leaves and thus in photosynthesis rate per unit leaf area and mass, and in the ratio of photosynthesis to respiration and senescence;

2) Improved water and nutrient supply to remaining leaves, resulting in increased growth rate or longer growing period;

3) Increased photosynthetic efficiency and reduced senescence of young regrowth leaves compared with older leaves removed;

4) Increased allocation of photosynthates, both previously stored and currently produced, to new leaf at the expense of non-photosynthetic roots, stems, and sometimes inflorescences;

5) Activation of dormant meristems in response to removal of apical meristems and/or modified light conditions, increasing the number of sinks for vegetative and eventually reproductive growth.

The existence of these mechanisms is extensively documented (e.g., reviewed by McNaughton 1979), as is largely acknowledged also by Belsky (1986).

These mechanisms of "compensating growth" are direct consequences of the morphology and physiology characteristic of plants, and in particular of their modular structure and plastic morphogenesis (Harper 1977), regulated by light and by concentrations of photosynthates, nutrients, and hormones. Plants in general are "preadapted" to regrow, repair, and, up to a point, compensate when their leaves and meristems are being

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removed by herbivores. Compensation need not be interpreted in every specific case as "coevolution with herbivores," but in some plants, selection under prolonged herbivore pressure may well have enhanced these responses.

The Net Effect of Grazing on Growth and Production

The net effect of grazing on plant growth and production is thus always the balance of counteracting effects: at least one negative (reduction of green area), and one or more positive effects. The balance depends on circumstances.

Most of the mechanisms by which plants compensate for losses to grazing can be expected to break down when the frequency and intensity at which individual plants are being grazed (or mowed) exceeds certain critical levels. Moderate reduction of leaf area will not affect—or will stimulate—growth in a dense canopy; but once grazing has reduced leaf area beyond a certain level, the plant is not able to replace leaves at the rate at which they are being removed (Noy-Meir 1975). Under frequent intensive grazing a similar "crisis" is expected to occur in the plant balance of meristems and nutrients, causing attrition and possibly death. If stimulation of production occurs at all in a particular plant–herbivore system, it is expected to occur at moderate grazing intensities, reaching a maximum and reverting to depression of production at higher intensity. This is the essence of the "grazing optimization hypothesis" (McNaughton 1979). Some plant species are able to tolerate higher repeated defoliation pressures than others, but every species has its critical limit.

The effect will depend also on the kind of grazer. Small-mouthed grazers (e.g., sheep, small antelopes, prairie dogs), which are able to graze plants down close to the ground and to pick leaves off stems, can easily depress plant growth. Compensating mechanisms should be effective at higher grazing intensities by cattle or bison, which are not capable of such close and finely selective grazing.

Thus, the direction and magnitude of the net effect of grazing on plant growth should depend entirely on conditions such as amount of green leaf area, number of meristems, amount of stored nutrients and assimilates, availability of soil resources, length of growing season, and frequency and intensity of defoliation.

The whole range of net responses, from negative through zero to positive, might therefore be found even in plants of the same species in different conditions, and indeed has been found in controlled experiments (Georgiadis et al. 1989, Maschinski and Whitham 1989). When results from different species in different environments are surveyed, widely diverging results are thus certainly expected. In grasslands, many studies have reported reduced production due to grazing, many others no effect, and some a moderate increase. There is good evidence for production increases in response to defoliation in some conditions in crops and forages, and there is no theoretical reason why it could not occur in productive grasslands. Every scientific result reported needs to be critically examined. There is no need to treat every report of "overcompensation" in nature either with special reverence (as the cornerstone of a new theory) or with special skepticism.

Individual vs. Community-level Effects

In many situations large herbivores do not graze individual plants but clip off patches containing many plants. The direct effect of grazing of an individual plant on its own growth is then compounded by the indirect effects due to the concurrent grazing of its conspecific or alien neighbors. The indirect effects, such as increased light intensity and reduced competing demands on soil resources, may often be as large, or larger, than the direct effects. Usually the indirect effects are likely to act in the positive, compensatory direction. The response that is then of ecological and evolutionary relevance is the overall effect of grazing on individual fitness, which results from the combination and interaction of direct and neighbor-mediated effects.

In the context of rangeland productivity, the relevant grazing effect is certainly the effect on community production.

What Production Measure?

Regrowth after grazing is predominantly of leaf tissue. Thus it may be expected that grazing will often increase or not affect leaf production, while at the same time reducing the accumulation of stem, root, and reproductive biomass. The empirical evidence from grasslands seems to support this as a broad generalization, even though in some cases removal of the primary shoot apex may stimulate secondary inflorescences to the extent that seed production is increased.

The effect of grazing on seed production per individual, a major component of fitness, is obviously of greatest relevance in the context of population dynamics and evolution.

The effect of grazing on total plant production (vegetative plus reproductive, both above- and belowground) is of some interest, but it has no greater ecological or evolutionary significance than the effects on components of production.

Relevance to the Use of Western Rangelands

Can all this help us to answer the practical question, how to use and manage rangelands in general, and those of "the West" in particular? The opening paper implies a choice between: (a) remove all cattle from public Western rangelands, or (b) extend the Savory intensive-grazing system to all Western rangelands. Obviously these two alternatives must be considered with reference to other logical options, like continuation of present management, or its modification in different ways.

The term "Western rangelands" covers a huge variety of climates, soils, vegetation composition, and productivity. The effect of grazing on rangeland productivity can thus be expected to vary within "the West" from substantially negative (e.g., in unproductive grassland grazed by sheep, starting early in the growing season) to substantially positive (e.g., in productive grassland grazed by cattle only in the period of rapid growth).

The effect of the livestock-grazing regime on the productivity of a particular rangeland is (or should be) of interest primarily to ranchers. The plant production that is relevant here is definitely that of aboveground edible biomass, and particularly of leaf, at the level of the community. However, the effect of the grazing regime on forage quality and utilization, species composition, and seasonality of supply is often just as important for animal production and economic success. In this wide sense, grazing optimization is a central concept of rational range management for production. Claims that a particular grazing system is superior in this context are relevant, but must be substantiated by critical experiments for each type of range.

From the point of view of other land uses and land values, and primarily conservation, the effect of livestock on grassland production is a marginal issue. The relevant questions here are: how does the presence, grazing intensity, and schedule of domestic herbivores affect vegetation structure, floral and faunal diversity, abundance and visibility of "interesting" wild animals and plants, soil structure, and incidence and intensity of fire? The answers to these questions in each range type are the crucial ones that research must provide, if it is seriously proposed to introduce a radical change like removal of livestock from large areas of public rangelands. Consideration of such questions has led to controlled livestock grazing being maintained, or reintroduced, in some grassland and woodland conservation areas in Israel and in Europe.

It is doubtful whether an intensified rotational grazing system, like the Savory system, has a chance of gaining acceptance on economic merits among range managers in large areas in the Western United States. If this were to happen, the consequences for other land values besides production would have to be examined by critical and long-term research in each range type.

Between these two extreme options (which right now happen to be promoted by enthusiastic protagonists), there are still several other grazing management alternatives that independent research may identify as preferable in this or the other type of Western rangeland, for production or conservation goals. Conservation and livestock grazing may turn out to be reconcilable in some rangelands, either locally, by multiple-use management, or regionally, by spatial diversification in management.

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