

GRAZING AND PLANT PERFORMANCE¹

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Abstract. Grazing is more than just defoliation of plants. The impact of herbivory affects ecosystem structure and function, both above and below ground. Ultimately, effects of herbivory are expressed to varying degrees at many levels of the ecosystem.

Herbivory has been shown to affect plant physiology, morphology, and genetics. Plants have evolved many ways to avoid or tolerate herbivory. Whether plants overcompensate, equally compensate, or undercompensate to herbivory depends on pre- and post-harvest conditions of the plants and their environment. To be important to the manager, the magnitude of compensation must be greater than the inherent "noise" in the system. Natural resources managers use scientific information about herbivory to reduce ambiguity in decision-making in an environment of uncertainty. If an ecological response like compensation is to have practical application for the manager, then meaningful effects must occur on time and spatial scales that the manager can respond to with available resources.

Key words: *compensatory growth; defoliation responses; grazing avoidance vs. tolerance; grazing resistance; hierarchical ecological levels; information needs of natural resources managers; plant fitness; plant physiological status; range management; semi-arid rangelands.*

INTRODUCTION

Grazing is more than just defoliation of plants. Large grazing herbivores change energy balance at the soil surface, create different levels of system disturbance, impact colonization of plants, remove and redistribute nutrients, and influence interactions with other kinds of animals. Ecologists have been primarily concerned with the defoliation aspect of grazing and with individual plant species responses to defoliation.

Most studies have used clipping or mechanical harvesting, rather than the grazing animal, to apply treatments. We have often assumed that defoliated plants respond in the same way as grazed plants (Trlica 1977). Rarely is this the case, as competitive background of the studied plant is usually also altered by the animal. We know from many empirical studies that clipping rarely can be used to simulate grazing. By clipping an individual plant and not neighbors, or vice versa, we make simplifying assumptions about intra- and inter-plant competition. Mueggler (1972) long ago showed how individual plants responded differently to different alterations in competitive background.

COMPENSATORY GROWTH AND OTHER RESPONSES

Two extremes exist on whether plants respond positively or negatively to herbivory. McNaughton (1976, 1979, 1983, 1984, 1986), Owen and Wiegert (1976), Dyer, Turner and Seastedt (1991), and others have pointed out that some level of defoliation or herbivory may result in overcompensation and may actually ben-

efit the plant that is utilized. Whereas a number of studies from agriculture systems and semiarid and arid rangelands have indicated that plants are often detrimentally affected by defoliation, and respond by undercompensation (Trlica 1977, Lacey and Van Poolen 1981, Whitham and Mopper 1985, Belski 1986, 1987, Painter and Belsky 1993), still other studies have shown that herbivores may have little effect on the plants on which they feed (Lee and Bazzaz 1980, McNaughton and Chapin 1985, Maschinski and Whitham 1989). These apparent contradictions have puzzled scientists and resource managers for years. Where does the truth lie? We propose that individual plants have quite plastic responses to herbivory, and that whether overcompensation, equal compensation, or undercompensation responses are measured after herbivory depends on a number of conditions experienced by the plant in the post-harvest period. All too often only aboveground components of plants have been studied, and interesting belowground phenomena ignored. If plants exhibit overcompensation in fruit or aboveground biomass production after being grazed at the expense of root growth, increased exudation, or reduction in depth of root penetration, what should this response be called, and what mechanisms are involved? We need to better understand whole-plant responses to herbivory and total plant carbon balance (Mooney 1972, Coyne et al. 1993).

Belsky (1986, 1987) suggested that an individual plant might exhibit overcompensation for herbivory under most favorable environmental conditions, but under less-than-favorable conditions this same individual might exhibit either equal compensation or undercompensation. This hypothesis was recently field tested by

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Maschinski and Whitham (1989) utilizing the monocarpic biennial species, *Ipomopsis arizonica*, where plants were subjected to varying levels of soil water and nutrient availability, interspecific competition, and defoliation. Their study illustrated a continuum of compensation responses in plant fitness (fruit set), depending on what phenological stage plants were defoliated, on nutrient and water regime, and on competitive background. They concluded that a plant probably will not compensate for herbivory as competition with neighbors increases, as nutrient availability decreases, and as the timing of herbivory comes later in the growing season. Overcompensation occurred only when grazed plants were supplemented with nutrients and were not competing with neighbors.

More studies like this one are needed to test other organisms, such as grasses, where fitness may be more associated with biomass production, longevity, and asexual reproduction, rather than on a one-time seed production event.

More attention must be given to a plant's phenological and physiological status when treatments are imposed and responses measured, to determine level of compensation achieved. For compensation to occur, physiological and morphological constraints must be overcome, and adequate abiotic and biotic conditions must exist (Maschinski and Whitham 1989). Obviously, plant responses to herbivory are conditioned by past history, current environmental conditions, and interactions among biotic and abiotic components. A better understanding of these interactions is what is presently needed.

The linkage between compensation in plants and its effect on animal populations may be weak at best. As pointed out by May (1973) and reiterated in Crawley (1983), fluctuations in plant and animal populations may occur quite independent of each other. This is especially important on the time and spatial scales of concern to managers.

Plants respond in a multitude of ways to grazing. Their individual responses vary depending on growth form, species genetic capabilities, morphology, physiology, and phenology. The three most important, manageable variables that influence plant response to grazing are (1) the timing of the grazing event in relation to the opportunity to grow or regrow, (2) the frequency of defoliation of an individual plant and its neighbors, and (3) the intensity of use (i.e., the level of defoliation).

Plants cope with grazing by minimizing the probability of being grazed or rapidly replacing leaf area removed by herbivores (Trlica and Orodho 1989, Briske 1991). Individually, the risk to a plant, or its immediate neighbors, of being defoliated under moderate stocking levels is relatively low. However, as the incidence of patch-grazing increases, so does the probability of an individual being grazed. Morphological features and biochemical compounds can also influence accessibil-

ity and the probability of a plant being grazed. The capability for rapid regrowth is affected by the availability of meristems and by physiological status. Interactions among plant structure and function determine a plant's ability to respond to grazing.

Plant mechanisms to cope with grazing vary greatly among species, and are more important to resource managers than is compensation after foliage removal. Avoidance reduces the probability and severity of defoliation, whereas tolerance mechanisms facilitate growth after defoliation (Briske 1991). One or both mechanisms may be employed by a plant. Grazing tolerance may be exhibited by compensatory photosynthesis, by rapid leaf replacement, or through alteration in carbon allocation patterns. Avoidance results from physical (e.g., spines or growth form) or chemical (e.g., secondary compounds that deter herbivores or interfere with their metabolism) deterrents. However, the carbon costs associated with grazing avoidance are considerable.

A trade-off probably exists between grazing avoidance and competitive ability. Those plants that invest heavily in defenses may not be as competitive as plants that invest little in such mechanisms. So, which plant is more fit? Obviously, it will depend on future environmental conditions that the plant must endure, and if grazing or competition will be more prevalent in the future.

Belsky (1986, 1987) did a good job of clarifying the ecological hierarchy in which plants exist. What might be viewed to be detrimental at some lower level in the hierarchy, may actually be neutral or beneficial at some higher level (e.g., an individual plant may be detrimentally affected by grazing, but community-level production might be increased). Plants do not grow as isolated individuals, but rather as members of a population, community, and ecosystem. Grazing is also a hierarchical process. Interactions of plants and animals among hierarchical levels are governed by specific animal decision rules. Therefore, foraging behavior varies with the ecological scale (Senft et al. 1987).

Grazing management is aimed at altering intra- and interspecific competitive interactions. Whether an individual plant overcompensates, undercompensates, or equally compensates after being grazed is of little concern to the resource manager. Grazing-induced modifications in competitive interactions are eventually expressed in changes at the population level (Briske 1991). A decrease in basal area or density of a species results in a reduction in resource acquisition within the community by that species. A change in species composition then alters the quantity and quality of production and, ultimately, the allocation and flow of energy in the ecosystem. Thus, studies of individual plant responses to defoliation may lead to identification of vital mechanisms involved in conferring fitness, but these studies may be of little value to someone re-

sponsible for management at the ecosystem or landscape level of organization.

MANAGERIAL NEEDS AND ECOLOGICAL RESEARCH

Resource managers function in an environment of uncertainty, and natural resource problems are open-ended. These decision-makers use many sources of information; some are based on science, some on other values. This has, in some instances, resulted in a duality between science and management. The major reason managers use research information is to reduce the risk of making incorrect decisions. If a duality exists between ecological research and application, a concerted effort should be made to eliminate the gap.

Although theories provide important constructs for decision-making at strategic levels, they are not very helpful to the manager at the tactical and operational level. Which is the hierarchical level of interest to the manager? What the manager needs is a potpourri of principles or fundamentals that are applicable to specific conditions. Principles or fundamentals can be organized and applied at different hierarchical levels in the system. The information that is relevant is only one hierarchical level more complex than the question. Knowledge of the mechanisms of organismal and population response makes decision-making more efficient, but problems can be solved without knowing specific biological mechanisms. Sometimes empirical relationships are as valuable as mechanisms to a manager. What may be scientifically interesting to an ecologist, may be of little consequence to the manager, and vice versa. If an ecological response, like compensation, is to have practical application, the magnitude of the effect must be greater than the intrinsic noise in the system, and the effect must occur on time scales to which a manager can respond with resources and labor that is available.

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