

North American terrestrial grazing

Pastoreo terrestre en Norteamérica

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ABSTRACT

This paper reviews four major aspects of North American herbivory:

(1) Plant antiherbivore chemical defenses. Complexes of secondary metabolites, which are repellent to herbivores, reduce fecundity and/or survival, or retard development, are present in the tissues of most plant species. They may shape foraging preferences more than nutritional needs. Herbivores can evolve resistance mechanisms, and resistant species tend to have narrow feeding specializations. The great variation in secondary-metabolite content between plant tissues, between seasons and stages of growth in individual plants, between plants of the same species, and between species is considered to be an adaptation to offset the evolutionary disadvantage which long-lived plants face *vis-a-vis* short-lived herbivores. Many plant species conserve their resources by producing little or no secondary metabolites until attacked by herbivores, and some appear to communicate the fact of attack to neighboring plants perhaps through the release of airborne pheromonal substances.

(2) Compensation and the grazing-optimization hypothesis. Several North American authors emphasize the compensatory response of plants and vegetations to herbivory. A fed-upon plant may increase net primary production (NPP) by increasing photosynthetic rates of residual tissues; reducing leaf-senescence rates; increasing growth of leaves, tillers, or axial shoots; or when grazing removes older, less-active foliage and increases light intensity for more active ones. Other authors find little or no compensation, measure only a depression in NPP from herbivory, and suggest that where compensation occurs, it may be at the expense of plant fitness.

(3) Herbivore-vegetation cycles. Investigators working in Canada have implicated cyclic fluctuations in vegetation as being mutually linked to 10-year cycles in snowshoe hare populations, and one author has suggested that cycles in secondary-metabolites may be a further cause of these oscillations. Others have suggested similar causation of herbivorous insect cycles. Predator-prey models have been proposed as abstract representations of herbivore-vegetation oscillations. Depending on the parameters used in the models, the time series may continue in stable cycles, or undergo damped oscillations and settle on equilibria. The latter has been suggested as typical for an ungulate-vegetation system over time, and in the U.S. wild-ungulate management in national parks is based on this model.

(4) Terrestrial grazing and plant-community composition. Development by North American range ecologists of a conceptual framework representing the effects of herbivory on plant-community composition has evolved over time from an early concentration and terminology on the effects of cattle grazing on grassland succession. More recent research in other vegetation types, and with other species of ungulates, has shown profound lateral shifts in vegetation composition — from a predominance of grasses to domination by shrubs and trees, or from shrubland to grassland — which grazers, or browsers, respectively, can effect. Newer concepts envisage the plant species within a community embedded in a matrix of interspecific competition. Specialist herbivores place their preferred plant species at a competitive disadvantage, reduce their abundance, allow the other plant species to replace them. Generalist herbivores, or aggregates of specialist species, place a balanced feeding pressure on the vegetation and maintain community diversity if the pressure is not excessive. Range managers now experiment with combinations of herbivorous species — e.g. cattle and deer — to maintain a diverse vegetation.

Hopefully, future research and theoretical inquiry will reconcile the contradictions between these lines of investigation and integrate them into a coherent framework of herbivory theory.

Key words: Antiherbivore defenses, grazing compensation, herbivore-plant cycles, community composition, range management.

RESUMEN

Los tejidos de la mayoría de las plantas contienen complejos metabólicos secundarios que pueden reducir, ya sea la fecundidad y/o la supervivencia de los herbívoros que se alimentan de ellos. Estos complejos moldean las preferencias alimentarias en mayor grado que las necesidades nutricionales. Los herbívoros, por otro lado, pueden desarrollar mecanismos de resistencia. Especies resistentes tienden a mostrar estrechas especializaciones alimentarias. La gran variación en metabolitos secundarios entre tejidos vegetales, entre estaciones y estadios de crecimiento en plantas individuales, entre plantas de la misma especie y entre especies, es considerada una adaptación para contrarrestar la desventaja evolutiva que tienen las plantas de vida larga en comparación con la vida corta de muchos herbívoros. Ciertas especies vegetales conservan sus recursos a través de la producción de pequeñas cantidades de metabolitos secundarios o bien

mediante su producción al momento del ataque. Es más, algunas plantas son capaces de comunicar el hecho del ataque a plantas vecinas a través de la liberación de feromonas.

Varios autores norteamericanos han enfatizado la respuesta compensatoria de algunas plantas y de la vegetación a herbívoros. Una planta pastoreada puede incrementar su producción primaria neta (PPN) incrementando la tasa de fotosíntesis en tejidos residuales, reduciendo la tasa a la cual las hojas senescen o incrementando el crecimiento de hojas, tallos principales y laterales. Por otro lado, la remoción de tejido viejo, menos activo fotosintéticamente, favorece incrementos en la intensidad de luz recibida en las porciones más activas. Otros autores, por el contrario, encuentran poca o casi ninguna compensación y sugieren que cuando ésta ocurre lo hace a expensas de una reducción en la tasa de sobrevivencia y capacidad reproductiva de la planta bajo consideración.

Investigaciones en Canadá han revelado la existencia de una íntima ligazón entre fluctuaciones cíclicas de la vegetación y la que ocurre cada 10 años en las poblaciones de *Lepus canadensis*. En este contexto, otros investigadores han sugerido el ciclaje del contenido de metabolitos secundarios como mecanismo causal de las fluctuaciones en el número de herbívoros. Modelos depredador-presa han sido propuestos luego como representaciones abstractas de la oscilación herbívoro-vegetación. Así, y dependiendo del modelo usado, la serie de tiempo puede continuar ciclando en forma regular o bien exhibir oscilaciones bruscas para luego estabilizarse en el equilibrio. Esto último ha sido propuesto como la trayectoria típica para describir sistemas ungulado-vegetación a través del tiempo, y viene siendo usada en los parques nacionales de los Estados Unidos de Norteamérica para manejar ungulados silvestres.

El desarrollo de este marco conceptual por parte de los ecólogos en pastizales en Norteamérica ha evolucionado a través del tiempo y comenzó con estudios de los efectos del pastoreo por parte de especies domésticas en la sucesión de pastizales dominados por gramíneas. Investigaciones más recientes, en otros tipos de vegetación y con otras especies de ungulados, han revelado profundos cambios colaterales en la composición de la vegetación de una región dominada por gramíneas a otra con predominancia de arbustivas o viceversa, la cual es afectada por los hábitos alimenticios de los animales. Este nuevo enfoque visualiza a las especies vegetales dentro de una comunidad embebida en una matriz competitiva. Los herbívoros especialistas ponen a sus especies preferidas en desventaja competitiva, reducen su abundancia y permiten que otras especies las reemplacen. Los herbívoros generalistas, o agregados de especialistas, ejercen una presión balanceada y mantienen la diversidad ecológica a nivel de la comunidad. Los manejadores de pastizales experimentan ahora con combinaciones de herbívoros, e.g., vacunos y venados, en su afán por mantener el balance dentro de la comunidad.

Palabras claves: Defensas anti-herbívoro, compensación de pastoreo, ciclos herbívoro-planta, composición comunitaria, manejo de praderas.

INTRODUCTION

When viewed in any kind of global perspective, terrestrial herbivory assumes virtually inscrutable complexity. We are confronted with the prospect of what will eventually prove to be several million species of herbivores feeding on some hundreds of thousands of plant species. One or more of the herbivorous species feed on each of the many plant tissues and organs by clipping, mining, rasping, sucking, rolling, boring, chewing, galling, tunnelling, etc.

The degree of effect ranges over a spectrum, depending on the tissues attacked, and the densities and species composition of the attackers. The effects can be investigated at several levels of mechanism and integration: (1) Effects on the physiology and morphology of individual plants. (2) Effects on the demography of single-species populations. (3) Effects on plant community composition. (4) Effects on plant evolution.

The process is, of course, interactive with the plants affecting the animals, both positively and negatively, over a scale of mechanisms: (1) The animals' nutrition, physiology, and morphology. (2) The dynamics of single-species populations. (3) Animal community com-

position. (4) The herbivores' evolution.

Together, the interactions between the two trophic levels importantly shape ecosystem structure and function. A complete review of North American research on terrestrial herbivory would address each of these eight topics in detail. However, that would be beyond the time and space limits of this workshop. I have chosen instead to touch on four of the more recent and active research areas which have stimulated considerable interest among North American ecologists. In all cases they have a strong basic ecological focus, but have important applied implications as well.

PLANT ANTIHERBIVORE CHEMICAL DEFENSES

Secondary Metabolites

We have long been aware of such plant morphological defenses against herbivores as thorns, trichomes (Levin 1973), prostrate growth form (Peterson 1962, McNaughton 1983a), and premature abscission of gall-bearing leaves (Williams & Whitham 1986). Agronomists have recognized for some time that different varieties of crop plants vary in their vulnerability to insect attack.

We have similarly known about the insecticidal properties of such plant extracts as rotenone, pyrethrum, and nicotine solutions. But it is only in about the last two decades that North American ecologists have become aware of the universality of chemical compounds in the tissues of plants which repel or poison herbivores in various ways. Most of the discoveries have involved plant-insect interactions, but others disclose effects on nematodes, molluscs, and mammals. Probably all groups of herbivorous animals are affected.

The research has expanded so fast that it has evolved into a new ecological subdiscipline called "chemical ecology" (Cates *et al.* 1983, Anonymous 1986). A large literature contains a number of synthesis volumes (cf. Rosenthal & Janzen 1979, Denno & McClure 1983, Hedin 1983) and review papers by Levin (1976) and Bryant & Kuropat (1980). The substances are commonly termed "secondary compounds" or "secondary metabolites" because they are derived from by-products of sugar and amino-acid metabolism in plants (Levin 1976). They generally fall within the following classes of compounds (Levin 1976, Rosenthal & Janzen 1979): Alkaloids; cyanide and cyanogenic glycosides; flavinoid pigments; glucosinolates; insect hormones and antihormones including steroids; nonprotein amino acids; phenolics; phytohemagglutinins; proteinase inhibitors; quinones; saponins; sesquiterpene lactones and other terpenoids; tanins and lignins; toxic seed lipids; waxes. Among the many plant species in which these have been identified, the actual chemical configurations vary so widely that thousands of compounds have been described, including more than 4,000 alkaloids alone (Levin 1976). They occur in every plant tissue, sometimes singly, but more often in varying combinations.

An abundance of evidence bears witness to their value to plants in protecting against herbivorous attack. Thus, Cates *et al.* (1983) found, in studying Douglas fir (*Pseudotsuga menziesii*), that 50 percent of the variation between trees in spruce budworm infestation (*Choristoneura occidentalis*) was associated with variation in the kinds and amounts of terpenes in the foliage. Louda & Rodman (1983) found an inverse correlation between the isothiocyanate-yielding glucosinolate (IYG) con-

tent of leaves from the cruciferous forb *Cardamine cordifolia*, and the amount of insect damage. So profoundly do these substances appear to determine the distribution on, and use of, plants by herbivores that numerous authors are converging on the view that feeding activity is guided more by the presence or absence of chemicals than by the animals' search for nutritional needs (Ehrlich & Raven 1964, Freeland & Janzen 1974, Cates & Orians 1975, Bryant & Kuropat 1980, Bryant 1981). The generalization is being extended both to invertebrates (Berenbaum 1981) and vertebrates, Bryant & Kuropat (1980) suggesting the relationship for seven species of gallinaceous birds, two species of hares (*Lepus* spp.), moose (*Alces alces*), and beaver (*Castor* sp).

Effects on Herbivores

Some of the compounds work as repellents, and deter attack in this manner. Those which are ingested may act as actual toxins; others are digestion inhibitors which impede enzyme action or inactivate gut microorganisms. Effects on herbivores may include actual mortality, reduced fecundity, or retarded development. Some species never complete metamorphosis.

Rhoades (1979) reviews some of the mechanisms which herbivores have evolved to circumvent plant defensive chemistry. Some detoxify the compounds variously by oxidation, reduction, hydrolysis, and chemical combination of two or more toxic compounds into nontoxic substances. Others sequester the materials and excrete them unchanged. Still others use them, or their own modifications, as defenses against predators and parasites.

Although several studies have found no differences between specialists and generalists (cf. Moran 1986), those herbivores which are most resistant to secondary compounds tend to be specialists which feed upon a narrow range of host species (Rhoades 1979). Generalist feeders appear to be less resistant and are forced to search out plant species with lesser chemical defenses (Berenbaum 1981, Zucker 1983). The implication seems to be that adaptation for resistance to any given compound is demanding on the herbivore, and its resources are not sufficient to allow adaptation to a wide range of them. This enhances the importance of chemical variability in plants.

The Importance of Chemical Variability

One of the recurring themes in the writings of the chemical ecologists is the extreme variation in amounts, kinds, and combinations of secondary compounds which they find within and between plants. Concentrations may vary within individual plant organs. Thus Zucker (1982) found a gradient of increasing phenol concentration from the base to the tips of *Populus angustifolia* leaves. This correlated with aphids' (*Pemphigus betae*) preference for forming galls near the base rather than farther out on the leaves.

Secondary-compound content also varies between organs on the same plant. Bryant (1981) found higher resin content in young shoots of willow (*Salix* sp.) and aspen (*Populus tremuloides*) than in the branches of mature trees. Whitham (1983) found a 42-fold, between-branch difference in the number of aphid galls on *P. angustifolia*. This indicated marked differences between phenolic content of branches on the same tree. Rodman & Louda (in press) found differences in IYG concentrations between roots, stems, basal leaves, and cauline leaves of *Cardamine cordifolia*. Chemical compounds also vary seasonally within the same plants (Janzen 1979, Schultz *et al.* 1982).

Within a given plant species, between-plant differences are especially pronounced (Dolinger *et al.* 1973, Schultz *et al.* 1982, Rodman & Louda in press). Whitham (1983) found a 146-fold, between-tree difference in aphid infestation of *Populus angustifolia* which he inferred was an indication of commensurate differences in chemical defenses.

The between-species variation in types and concentrations of compounds, and combinations thereof, is equally pronounced (Dolinger *et al.* 1973, Bryant 1981, Schultz *et al.* 1982). Berenbaum (1981) surveyed the furanocoumarin content of 12 species of Umbelliferae in New York. Those containing the substances were species of open habitats, while woodland species characteristically lacked them. This correlated with the phototoxicity of furanocoumarins to insects.

These variations have generally been considered to be adaptive strategies on the part of the plants. Mc Key (1974) and Bryant & Kuropat (1980) have suggested that the within-plant variation is

adjusted to protect those parts on which herbivore attack would most severely affect the plant's fitness. Several authors (e.g. Cates & Orians 1975, Bryant & Kuropat 1980, Schultz *et al.* 1982, Bryan *et al.* 1983, Cates *et al.* 1983) have shown secondary-compound content of late-successional plants to be higher than that of pioneers and ephemerals, and suggested that the volatile demography and short lifespan of early-successional forms places them at less of an herbivore risk than the long-lived constancy of late-seral perennials.

But in a more general perspective, Whitham (1983) has pointed out that, on a demographic basis, long-lived perennials are at an evolutionary disadvantage with their short-lived herbivorous attackers. By virtue of rapid generation turnover, the latter potentially can evolve protective responses faster than the plants can evolve defenses, and the latter are therefore at continuous risk of losing protection.

The variability and diversity of secondary compounds is suggested to be the answer to this demographic disadvantage (Dolinger *et al.* 1973, Levin 1976, Rhoades 1979, Schultz 1983, Whitham 1983, Zucker 1983). An insect may, after several generations, adapt to the chemistry of a given plant or plant part. But if this chemistry changes in time, the animal loses its advantage. And if the chemistry of neighboring plants differs from that of an insect's host, neither it nor its offspring will have gained any advantage. As noted above, insects may evolve resistance to some toxins while not doing so to others.

Moreover, Whitham (1983) surmises that the variation in plant defenses between leaves and branches of *Populus angustifolia* forces aphids (*Pemphigus betae*) to concentrate on those leaves and branches where defenses are lowest and/or nutrition is highest. In concentrating, they become more vulnerable to intraspecific competition. Reproductive females on leaves with only a single gall produce 90 progeny each per year. But where two females settle on a single leaf, the average progeny per female is 59. The concentration also increases aphid mortality. Leaves with two or more galls are more likely to abscise prematurely and kill the aphids on them than are leaves with only a single gall (Williams

& Whitham 1986). Schultz (1983) and Whitham (1983) also suggest that concentrating attracts predators.

These risks may have, according to Whitham (1986) selected for territorial behavior by the aphids which defend territories on the most favorable areas of the leaves and attempt to prevent other females from becoming established. In this way, and by forcing adaptation to the plants' variable defenses, they may manipulate the evolution of their predators (Whitham 1983).

Dolinger *et al.* (1973) have attributed the susceptibility of cultivated plants to the artificial selection for productivity which likely comes at the cost of trading off secondary-metabolite production; and to the genetic uniformity of cultivated plants.

Optimal Defense Theory

The findings from secondary-metabolite research have been further embedded in evolutionary theory by Rhoades (1979). He suggests that, in producing these compounds, the plant draws on resources that it would otherwise allocate to other functions. There is thus a cost to these functions, and ultimately to plant fitness.

That the plant's resources are limited, and must at times be allocated to certain functions at the expense of others is shown by the effects of stress on secondary-metabolite production. Several investigators (cf. Rhoades 1979, Cates *et al.* 1983, Louda & Rodman 1983) have reported that plants under environmental stress contain lower concentrations of secondary metabolites and/or sustain higher levels of herbivore attack. Louda (in press) showed increases in attacks by three insect guilds on *Cardamine cordifolia* plants on which she had severed roots, had transplanted, and had subjected to flooding. She surmised that attack by one form of herbivore would make it vulnerable to attack by others.

The plant is thus faced with the need to protect itself from herbivore attack, but at the lowest possible level to avoid trade-offs of resources needed for other survival needs. Plants apparently meet this need by not, or minimally, producing secondary-compounds until attacked: in essence, the herbivore *induces* metabolite production and concentration. Thus Do-

linger *et al.* (1973) found alkaloid concentrations low in the flowers of three species of *Lupinus* where the lycaenid butterfly *Glaucopsyche lygdamus* was scarce. But where *Glaucopsyche* was abundant and preying intensively on *Lupinus*, the flowers contained high concentrations of nine alkaloids. Green & Ryan (1972) report accumulation of proteinase inhibitors in leaves within hours after they were bitten by herbivores or artificially damaged to simulate insect attack. Schultz & Baldwin (1982) found tannin and phenolic concentrations higher in the leaves of red oaks (*Quercus rubrum*) that had been defoliated the previous year by gypsy moths (*Lymantra dispar*) than in undefoliated trees.

One of the discoveries that has created considerable interest is the apparent ability of some plants to communicate the fact of herbivore attack to their neighbors. Rhoades (1983a), in studying the effects of tent caterpillar (*Malacosoma californicum pluviale*) and webworm (*Hyphantria cunea*) attack on red alder (*Alnus rubra*) and Sitka willow (*Salix sitchensis*) observed induced changes in leaf quality. Moreover, similar changes were observed in nearby *Salix* plants not attacked by the insects, and known not to be attacked by roots to the infested plants. Baldwin & Schultz (1983) observed similar phenomena between potted seedlings — some artificially damaged and some maintained as controls — of *Populus x euroamericana* and *Acer Saccharum*. These investigators surmise that the communication occurs through airborne pheromonal substances.

COMPENSATION AND THE GRAZING-OPTIMIZATION HYPOTHESIS

By far the prevailing ecological stereotype of herbivory in North America has been of an interaction that is favorable to the eater, but detrimental to the eaten upon. A large number of studies have measured the effects of herbivorous removal on the physiology, growth, reproduction, survival, and composition of individual plants, plant species, and plant communities. The underlying perspective on the secondary-metabolite work that we have reviewed is to consider these compounds as

protection against the deleterious effects of herbivores on plants.

A sample of recent North American papers includes Foster & Stubbendieck's (1980) observations that plains pocket gophers (*Geomys bursarius*) consistently reduce production of herbaceous vegetation in areas in which they were studied. Cates *et al.* (1983) report that productivity of Douglas fir trees in their study was inversely correlated with the level of spruce budworm infestation. Louda (1984) measured increases in height and fruit production of *Cardamine cordifolia* plants when leaf-feeding chrysomelid beetles, *Phaedon* sp. nr. *oviformis*, were excluded. Whitham & Mopper (1985) found that pinyon trees (*Pinus edulis*) with low infestations of the stem- and cone-boring moth *Dioryctria albovitella* produced 47 percent more trunk wood and 43 percent more branch wood. Annual shoot production was reduced 30 percent in more heavily infested trees, and these were converted to functional males as they lost their ability to bear female cones.

Contrary to the prevailing view that herbivores negatively affect plants, a small number of investigators have begun to emphasize the positive effects, other than pollination and seed distribution, of herbivores on plants. Wildlife and range managers have for some years clipped plants experimentally to simulate varying intensities of grazing and browsing by large mammals. These studies have either shown that they can withstand significant levels of removal and continue to produce herbage (Aldous 1952, Krefting *et al.* 1966), or that they actually increased production (Garrison 1953, Willard & McKell 1978).

More recently, McNaughton (1979, 1983b) working in East Africa, and Hilbert *et al.* (1981), Dyer *et al.* (1982), and coworkers in North America, have begun to stress the compensatory responses of grassland productivity to grazing by wild and domestic ungulates. Under certain conditions, total vegetative production is said to exceed (*i.e.* overcompensate) that which prevails in the absence of herbivory. Dyer and coworkers (Hilbert *et al.* 1981, Dyer *et al.* 1982) have proposed a graphical optimization model (Fig. 1) which in their view represents the degree to which above-ground net primary pro-

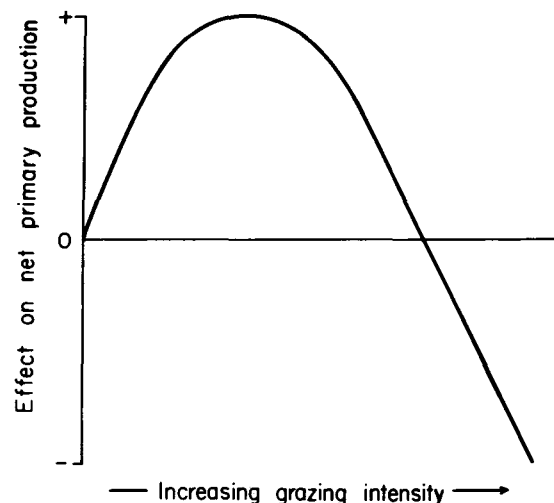


Fig. 1: Hypothetical grazing-optimization curve (after Dyer *et al.* 1982) which proposes that net primary production is increased by grazing up to a certain intensity. Beyond this point, the enhancement is progressively less until, at some point of heavy grazing, production is suppressed below that of ungrazed vegetation.

Curva hipotética de optimización en respuesta al pastoreo (Dyer *et al.* 1982), la cual propone que la producción primaria neta se incrementa hasta cierto nivel de intensidad de pastoreo. Después de este punto, el incremento se hace progresivamente menor hasta que en cierto punto, bajo pastoreo intenso, la producción es depurada por debajo del nivel correspondiente al de la vegetación no pastoreada.

duction (NPP) is increased or decreased at different grazing levels.

Range managers have been quick to embrace this concept both as a potential means of setting optimal stocking rates for livestock, and because it provides a basis for arguing that livestock grazing can actually benefit vegetation. Some ecologists go so far as to suggest that herbivory is actually a mutualistic relationship (Mattson & Addy 1975, Owen & Wiegert 1976), and that consumers maximize plant fitness (Owen & Wiegert 1976).

Although criticized on methodological grounds by Belsky (1986), McNaughton's (1979) has been the most convincing evidence of strong overcompensation. In areas that had been subjected to moderate grazing by wildebeest (*Connochaetes taurinus albojubatus*), the NPP was twice as great as that in an ungrazed enclosure. Some increase in NPP was evident over most intensities of grazing; and even at the heaviest intensity, NPP was no lower

than that in the enclosure. He attributed such overcompensation to one or more of nine mechanisms: (1) Increased photosynthetic rates in residual plant tissues. (2) Reallocation of substances from elsewhere in the plant. (3) Mechanical removal of older tissues functioning at less than a maximum photosynthetic level. (4) Increased light intensity upon potentially more active underlying tissues. (5) Reduction of leaf-senescence rate, thereby prolonging the active photosynthetic period of residual tissues. (6) Hormonal stimulation of leaf growth and tillering. (7) Conservation of soil moisture by reduction of transpiration surface. (8) Nutrient enrichment from dung and urine. (9) Direct growth stimulation by components in ruminant saliva.

Attempts at making a similar case for an increase in NPP in North American grassland vegetation have not been as persuasive. There is evidence for some of the above compensatory mechanisms. Dyer *et al.* (1982) review a number of cases in which the photosynthetic rate in residual leaves of grazed plants is higher than in similarly positioned leaves of the same age in ungrazed plants, and of increased tiller growth in grazed plants. Nowak & Caldwell (1984) also observed increased photosynthetic rates in residual tissues of clipped *Agropyron desertorum* and *A. spicatum* grasses, as well as a delay in senescence of residual leaves.

Reardon *et al.* (1972) measured an increase over controls in forage yield of side-oats grama grass (*Bouteloua curtipendula*) clipped and treated with bovine saliva. Greenhouse plants of the same species showed a 232 percent increase in forage yield when given a soil application of thiamine, a substance occurring in bovine saliva. But Detling *et al.* (1980) were unable to get a similar response with North American bison (*Bison bison*) saliva applied to *Bouteloua gracilis*. Dyer & Bokhari (1976) inferred a stimulatory effect on *Bouteloua gracilis* growth in the laboratory when fed upon by grasshoppers (*Melanoplus sanguinipes*), but clipping leaf blades to simulate grasshopper removal reduced net photosynthetic rates in those blades (Dyer *et al.* 1982). These authors also have explored the presence of plant growth factors in mouse submaxillary glands, but the results are inconclusive.

Moreover, the evidence for effects of herbage removal on total NPP is highly variable. Willard & McKell (1978) observed a 30 percent increase in total herbage production of two shrub species, *Chrysothamnus viscidiflorus* and *Symphoricarpos vaccinioides*, from which twigs had been clipped. But most of the examples reviewed by McNaughton (1983b) found some reduction in productivity from defoliation, the compensatory mechanisms operating to make the damage less than proportional to the degree of herbage removal. Several authors report an initial increase in growth from clipping experiments (cf. Garrison 1953, Jameson 1963) and herbivorous attack (Windle & Franz 1979) followed by a later decline.

Other authors find little or no compensatory response. Cook (1971) found some reduction in plant vigor among desert shrubs, perennial grasses, and suffrutescent half shrubs after experimental removal of as little as 25 percent of the current annual growth. Lacey & Van Poolen (1981) review the findings of 11 studies in six states on the effects of moderate and no livestock grazing on NPP. Herbage production in the ungrazed vegetation averaged 68 percent higher than in the moderately grazed. In three clipping studies on individual plants reviewed by these same authors, production of unclipped plants averaged 59 percent higher. While finding evidence of limited compensatory photosynthesis in their clipping studies of two grass species, Nowak & Caldwell (1984) concluded "... compensatory photosynthesis does not appear to be an important ecological component of herbivory tolerance for these species".

Janzen (1979) cautions that a given plant response cannot automatically be assumed to improve fitness. A compensatory vegetative response could occur at the expense of other processes importantly affecting plant fitness. Indeed, numerous investigations have found a reduction in root mass in response to defoliation (Jameson 1963, Willard & McKell 1978, Windle & Franz 1979, Richards 1984), a change that could well impair the plant's ability to compete with neighbors. Garrison (1953), Jameson (1963), and Willard & McKell (1978) report a reduction in flower, fruit, and seed production following compensatory growth.

In total, the question of when and if a compensatory response occurs appears to be an open one. After a detailed review, Belsky (1986) goes so far as to conclude that there is no convincing evidence to support the theory that herbivory increases NPP. The same doubts appear to hold for the extent to which the plant makes a trade-off between compensation and other functions affecting its fitness. As McNaughton (1979) has pointed out and I have reviewed above, there is a broad complex of plant physiological processes which may or may not compensate. Subtle differences in these processes between species may determine whether or not they are tolerant or sensitive to grazing, and whether or not there is compensation in NPP.

Thus Caldwell *et al.* (1981) and Richards (1984) have shown that, following defoliation, the grazing-tolerant Eurasian grass, *Agropyron desertorum*, accelerates reformation of its canopy and curtails root growth. The closely related North American *Agropyron spicatum*, which is grazing-sensitive, reforms its canopy much more slowly, but continues with root growth unabated. It is not until the following year that an increase in root mortality begins to restore a balanced shoot: root ratio. Meanwhile, *A. desertorum* achieved the balance in the year of defoliation with its vegetative and root-growth patterns, and consequently does not experience the increased root mortality in the second year. But in neither case is there significant NPP compensation (Nowak & Caldwell 1984) as mentioned above.

An interesting paper by Inouye (1982) typifies the problem of generalization very well. The thistle, *Jurinea mollis*, is fed upon in three ways by different species of herbivores, and each way elicits a different response from the plant. First, when lepidopteran larvae eat the central part of the basal rosette, multiple rosettes are produced on a single root. Plants with multiple stalks can produce up to three times as many seeds as those with single stalks. Up to half of the flowering plants in his study area had multiple stalks. Secondly, the terminal flower heads of some plants are removed by some unknown herbivores, probably small mammals. The plants respond by developing axillary flower heads which are much less successful

than terminal heads at producing seeds. Thirdly, moths and tephritid flies damage the flower-head receptacles which interrupts seed development. There is no apparent response by the plants, which may produce no viable seeds.

An investigator looking at only one of these interactions might be prompted to conclude, depending on the one examined, that herbivory (1) elicits compensation and increases fitness, (2) elicits compensation but at the cost of reducing fitness, or (3) elicits no compensation and reduces fitness.

HERBIVORE-VEGETATION CYCLES

Animal ecologists have long been interested in cyclic fluctuations of animal populations, one category of which is mutually induced predator-prey cycles. In recent years, the suggestion has been made on both theoretical and empirical grounds that herbivores and vegetation may cycle in ways that are analogous to predator-prey systems, the focus simply being lowered by one trophic level.

Empirically, one of the strongest examples has been reported by Keith and coworkers (Keith & Windberg 1978, Pease *et al.* 1979) who studied 10-year population cycles of snowshoe hares (*Lepus canadensis*) in southwestern Canada in the 1960s and early 1970s. Based entirely on their field observations of hare demography and vegetation, these investigators concluded that the hare cycles were induced by changing availability of vegetation. The vegetation changes, in turn, were caused by alternate heavy use during periods of hare abundance, and light use during hare scarcity at which time the vegetation could regrow. The critical food was the vegetation used in winter which consisted primarily of small twigs of shrubs and young deciduous trees within reach of the animals.

May (1973) has shown that the insertion of a time-delay into simple population equations can induce oscillations into a population trajectory. Bryant (1981) proposed just such a time delay for vegetation fed upon by snowshoe hares. He measured resin content in young regrowing root suckers of the deciduous species fed upon by hares in Alaska. For

about 3 years after first appearance, these shoots had extremely high resin content, and were not palatable to hares. After about the third year, the resins declined and the shoots once again provided winter hare food. Bryant suggested this as a possible cause of the hare cycles. Rhoades (1983b) suggested similar causation of herbivorous insect cycles, possibly induced by oscillations in secondary metabolites.

North American investigators studying forest insects have described what in essence are herbivore-vegetation cycles operating over a much longer time frame. The eastern spruce budworm, larva of the moth *Choristoneura fumiferana*, has been studied for decades by a team of investigators in southeastern Canada (cf. Morris 1963, Royama 1981, 1984). The species is quite inconspicuous, even rare, in the early and intermediate seral stages of the taiga, and has no significant influence on the forest vegetation. But the late-successional stages provide a habitat structure that reduces the levels of mortality incurred by the larvae in the early seral stages, while at the same time not containing adequate biotic checks on budworm populations. At this point, a fortuitous series of favorable weather years allows the species' populations to explode into epidemics which defoliate and kill the conifers, and set the vegetation back to the pioneer stage.

A very analogous situation has been described for the effects of mountain pine beetle (*Dendroctonus ponderosae*) on lodgepole pine (*Pinus contortus*) forests in western U.S.A. (Roe & Amman 1970, Cole 1973, 1975, Cole *et al.* 1976). Beetle populations in young forests occur at relatively low densities and damage few pine trees. But when the trees mature to about 25-30 cm diameter at breast height, beetle epidemics break out. The phloem layer around the trees is girdled, and entire forest stands are killed. If there is no understory of young, late-successional conifers (lodgepole pine is an early-seral species), the forest is returned to the pioneer stage.

Both of these examples are essentially successional ones, with a time scale measured in decades. The vegetation is at first unaffected through most of the sequence, then eliminated in a short period of time by an herbivore which has been held in check for most of the

sequence, then suddenly freed from constraint.

May (1973) and others have analyzed the stability properties of two-trophic-level models with the hope of deducing the general principles of dynamic behavior in trophic interactions. Like others, he began with the Lotka-Volterra predator-prey model which produces cyclic behavior in the two components. This representation of a two species system is excessively simplistic, but is a structural starting point for the more realistic models of most authors:

$$\frac{dH}{dt} = H(b_H - d_H P) \quad (1a)$$

$$\frac{dP}{dt} = P(b_P H - d_P) \quad (1b)$$

where H and P are the numbers of prey and predators, respectively, at time t , b_H and b_P are the respective birth rates of prey and predators, and d_H and d_P are the death rates of the two species.

The major ways in which the equations are unrealistic representations of real populations are: (1) in the absence of any predators, the prey increase without limit; (2) a predator kills a constant fraction of prey regardless of how many prey there are; and (3) the predators increase without limit as long as prey numbers continue to increase.

May (1973) proposed an alternate set of equations which Caughley (1976) and Crawley (1983) have taken to represent a herbivore-vegetation system. These are in my notation and slight rearrangement of the second equation to show the parallel with the Lotka-Volterra equations, as follows:

$$\frac{dV}{dt} = b_V V (1 - \frac{V}{K_V}) - d_V H (1 - e^{-g_1 V}) \quad (2a)$$

$$\frac{dH}{dt} = H(b_H(1 - e^{-g_2 V}) - d_H) \quad (2b)$$

Where V is vegetation biomass at time t , b_V is the vegetation growth rate, K_V is the greatest standing crop to which the vegetation can grow (its "carrying capacity"), the second half of the first equation is the rate of vegetation con-

sumption by the herbivores with g_1 , the slope of the function, g_2 the slope of the herbivore growth curve, and e the base of the natural logarithms. The other terms are the same as in the Lotka-Volterra equations.

May (1973), Caughley (1976), and Crawley (1983) have shown that the nature of the time series generated by these models varies, depending on the actual values used for the parameters. If b_v is small and/or K_v large, the system will undergo self-sustaining cycles. But if b_v is large and/or K_v is small, the system will oscillate at first, but the cycles will damp out and settle on stable equilibrium points. Still other values will move the system directly to equilibrium.

To what extent these models abstractly simulate real-world herbivore-vegetation systems remains to be determined. I have suggested (Wagner 1981, in press) that real populations may fall along a continuum between Models (1) and (2), and that Keith's snowshoe hare-vegetation cycles may be represented by a model approaching (1) although the data series was not long enough to see whether or not there is a good fit.

In considering the range of dynamic behavior which Model (2) can exhibit, Caughley (1976) argued on a purely evolutionary rationale that both equilibrium-point and cyclic behavior are unlikely for real world herbivore-vegetation systems. Hence, oscillations damped to equilibrium points seemed to him the most likely. He then selected (Caughley 1976, Caughley & Lawton 1981) a set of values for the parameters in the equation that first generate an irruption by the herbivore and a sharp drop in the vegetation. Subsequently both go through damped oscillations until they reach respective equilibria. The level for the herbivore he termed the "ecological carrying capacity" (Caughley 1976, 1979).

The herbivore population can be held at equilibrium at densities below the ecological carrying capacity by predators, hunting, and other factors. Hence, a range of equilibrium densities is possible, and the range is inversely related to vegetation biomass. Maximum offtake or yield of animals is possible at some intermediate density of animals and plant biomass, and Caughley has termed this animal

population level the "economic carrying capacity".

Caughley has proposed that this model and conceptual framework are appropriate first approximations for representing the behavior of large-ungulate-vegetation systems, both wild and domestic ungulates. Houston (1982:62) has embraced this scheme, and proposed further that "Ecological carrying capacity (K_1) characterized by a higher standing crop of animals and a lower standing crop of edible vegetation, is usually the level that is relevant in national parks". The conclusion supports the current wildlife-management policy of the U.S. National Park Service which proscribes human intervention, and advocates a *laissez-faire* approach to the biota, left free to interact and seek its own levels.

For the past 20 years, Yellowstone National Park has pursued this policy with the management of a large elk (*Cervus elaphus*) population (Houston 1982). Contending that the elk and vegetation have coexisted for millenia and must have reached Caughleyesque equilibria, Park policy advocates leaving the herd to seek its own equilibrium density and viewing the vegetation as being at equilibrium.

A number of observers outside the Park Service have grown restive over the situation, believing that they see evidence of vegetation deterioration that is causing the decline of other ungulate species. The subject has recently been reviewed in detail by Chase (1986) who has challenged Park Service policies.

Caughley & Lawton (1981) were cautious about the use of these models. They were, they point out, originally designed to represent the interaction of one predatory and one prey species. As herbivore-vegetation models, they imply one each herbivore and plant species, with the former feeding solely on the latter. As Caughley & Lawton note, this is quite unrealistic. And while large ungulates have feeding preferences, they do feed on a number of plant species, and in the absence of their preferred forms, will move to less preferred ones. Caughley (1982) provides a rationale for treating 2 and 3 plant species as a single one in his models, but (Caughley & Lawton 1981) remains cautious about the degree to which a single set of parameters can be used to simulate an n-species vegetation

comprised of annuals and perennials; of forbs, grasses, shrubs, and trees.

The models do appear to have heuristic value at this stage, but to base national-park management policies on them may well be scientifically premature and placing exceptional biotas at undue risk.

TERRESTRIAL GRAZING AND PLANT-COMMUNITY COMPOSITION

North American range ecologists have been concerned not only with the gross amount of forage produced by a given rangeland, but with the vegetative composition producing that forage. Different ungulate species have differing forage preferences, and the different plant species within the vegetation have differing nutritional values for each ungulate species. Hence, one of the range manager's primary goals has been to devise systems that allow a vegetative composition with maximum production by those plant species most nutritious for any desired ungulate species or combination of species. The latter may be domestic livestock or wild ungulates, or both.

The ecological problem is to understand how different grazing patterns influence plant-community composition. Pursuit of this understanding has proceeded under two somewhat different conceptual frameworks, ecologically.

The Successional Framework

In North America, the discipline of range management began developing around the turn of the century (Stoddart *et al.* 1975). But its plant-ecological basis was strengthened in the 1930s and 40s by close association with emerging ecological theory developed by F.E. Clements (1928) and J.E. Weaver (Weaver & Clements 1938). These investigators were particularly interested in the phenomenon of succession, and successional theory played an important role in emerging plant-community theory. While there was some general view that interspecific competition played a role in succession, with more competitive species replacing less competitive ones, the interest in competition nowhere assumed the emphasis it would receive in North American community ecology in the 1960s-80s.

The emphasis on plant succession carried over into the conceptual basis of range ecology. E.J. Dyksterhuis (1946, 1949) developed a formal, range-management terminology for the behavior of plant species under different grazing intensities which was in essence a successional scale. "Decreasers" are climax species which predominate in the absence of disturbance, and which decrease in abundance as the vegetation is grazed. Those species which initially increase in abundance as the decreaseers decline, and which may assume dominance under moderate grazing are termed "increasers". Under heavy and continued grazing pressure, the vegetation is driven to the pioneer successional stage where species termed "invaders" predominate. This terminology remains in the range-management lexicon today, and is in general use by contemporary range managers.

In the decades following Dyksterhuis' work, the range-management discipline also developed a scheme for grading the condition of rangelands. Generally, four condition classes—excellent, good, fair and poor—are recognized, and these correspond to successional stages ranging from climax to pioneer, successively. Some authors (*e.g.* Sims & Dwyer 1965) have combined the Dyksterhuis classification of species with the range-condition classification. A range in excellent condition contains a majority of decreaseers, and only minor percentages of increasers and invaders. A range in poor condition is composed largely of invaders, few increasers, and few or no decreaseers. Good and fair ranges have varying combinations of the three classes of species.

This phase of range management conceptual development took place largely in the central North American grasslands. Weaver's research concentrated on grassland ecology. Dyksterhuis' seminal work was carried out in Texas grasslands.

The result of this grassland emphasis was a somewhat linear and restrictive picture of the effects of ungulate grazing on vegetation composition for several reasons. First, the number of vegetative life forms in grasslands is often only two: grasses and forbs. Secondly, the studies leading to this early development concentrated on grazing by cattle, a species that prefers herbaceous vegetation, especially the graminoids. Third, palata-

bility and nutritional value of plant species for cattle in the grasslands are considered to be linearly correlated with successional status: climax perennial grasses the most palatable and nutritious, weedy invaders the least.

Hence, at this stage of conceptual development, the effects of grazing on plant-community composition were considered to be a function of the intensity of cattle grazing on grassland vegetation, and the corresponding degree to which it had been driven down the linear, successional scale.

The Competition and Diversity Paradigm

The pattern becomes more complex, however, when an herbivore-vegetation system contains (1) additional vegetative life forms (e.g. woody species, succulents), and (2) herbivorous specialists other than, or in addition to, cattle. Evidence for the complexity has emerged from research on domestic sheep and goats, and on wild deer (*Odocoileus* spp.); and on vegetation types other than grassland. The latter include the grassland-woodland ecotone of central Texas; the grassland-desert ecotone of west Texas, New Mexico, and Arizona; and the high desert and shrub steppe of the North American Great Basin. Much of the understanding has come from studies on experimental grazing areas in the western United States, where the effects of different grazing treatments on vegetation have been measured for periods as long as 50-75 years.

In vegetation types with significant amounts of woody species, like the above, cattle grazing commonly shifts vegetative composition to a predominance of shrubs and/or trees unpalatable to cattle. Semi-arid and arid North American rangelands have undergone extensive and profound changes of this type. Gardner (1951), Hastings & Turner (1965), Humphrey (1968), York & Dick-Peddie (1968), and others have described the change from desert grassland in Texas, New Mexico, and Arizona to shrub-dominated desert types. Farther north in the sagebrush (*Artemisia tridentata*)—grass vegetation of the northern Great Basin, heavy cattle grazing has reduced the perennial grasses and forbs, and increased the shrubs, particularly sagebrush (Fautin 1946, Pechanec 1949, Pearson 1965, Laycock 1967).

In some vegetation types, grazing-induced changes may not be evident to casual view. But floristically, they may be as fundamental as the above. Thus, in the salt-desert-shrub type of the Great Basin, grass is a minor component. The major species are low shrubs, suffrutescent half shrubs, and a few perennial forbs. This type has been primarily used for sheep grazing. Studies at the U.S. Forest Service's Desert Experimental range in southeastern Utah (Hutchings & Stewart 1953, Holmgren & Hutchings 1972) have shown that, under heavy grazing *Artemisia spinescens* and *Ceratoides lanata* are grazed out and replaced by *Atriplex confertifolia* (Fig. 2). The latter is similar in stature and general appearance to the other species, so the appearance of the vegetation does not change greatly. But it is of much lower forage quality.

So far, the emphasis has been on the effects of grazing species. But browsers, which prefer woody vegetation, can make

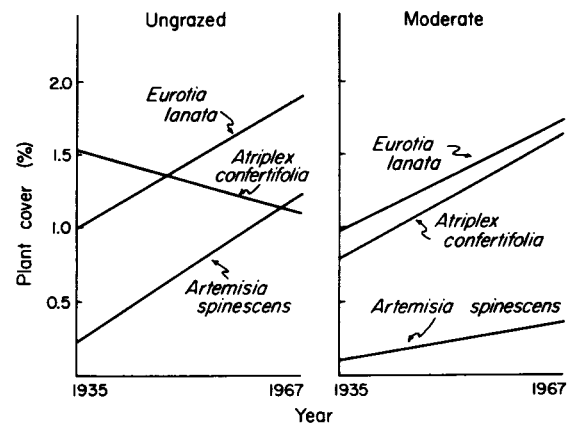


Fig. 2: Vegetation changes under moderate and no winter sheep grazing on salt-desert-shrub vegetation in southwestern Utah (after Holmgren & Hutchings 1972). Without grazing, the palatable *Ceratoides lanata* and *Artemisia spinescens* increase markedly while the unpalatable *Atriplex confertifolia* declines. Under moderate grazing, *Atriplex* increases while the palatable species increase less profoundly.

Cambios en la vegetación bajo pastoreo moderado y ausencia de pastoreo por ovinos durante el invierno en el desierto salado tipo arbustivo del suroeste de Utah (de acuerdo a Holmgren & Hutchings 1972). En ausencia de pastoreo, los arbustos palatables *Ceratoides lanata* y *Artemisia spinescens*, se incrementan marcadamente mientras que el arbusto no palatable *Atriplex confertifolia* declina. Bajo pastoreo moderado, *Atriplex* se incrementa, mientras que las especies palatables incrementan en menor cuantía.

changes in vegetation composition that range all the way from the suppression of individual plant species to complete alteration of vegetation type.

In the first category is the removal of certain palatable plant species from the vegetation by rising deer populations (Leopold *et al.* 1947). Austin & Urness (1980) and Urness (personal communication) have concluded that browsing by mule deer (*Odocoileus hemionus*) continually removes the reproductive saplings of curl-leaf mahogany (*Cercocarpus ledifolius*) in the mountains of northern Utah. As the older plants die out and are not replaced, the species is gradually disappearing from the montane vegetation. McAuliffe (1986) has reported that abundance of the palo verde tree (*Cercidium microphyllum*) in the Sonoran Desert may be suppressed unless other shrubs are present to protect the young seedlings.

In the latter category, domestic goats and white-tailed deer (*Odocoileus virginianus*) convert shrubby vegetation in central Texas to a grassland, and are managed to accomplish this feat (Merrill n.d.).

In many areas of western North America, the mule deer is a browsing species which summers in the higher montane elevations and winters on the foothills. When the first Europeans arrived, mule deer were scarce, apparently because the vegetation was predominantly grasses on the foothills and mature forests on the mountains. But the settlers' cattle converted the foothill vegetation to shrublands, which improved the food and cover for mule deer, allowing them to increase sharply in the first half of this century. However, in the past 30-40 years, livestock numbers have declined, and deer browsing on shrubs is converting the vegetation back to a grassland (Smith 1949, Wagner 1978).

The effects of herbivores on vegetation composition depend in part on whether it is fed upon during its season of greatest sensitivity to grazing. Desert vegetation tends to be most sensitive during the growing season (Wagner 1980). Heavy grazing by sheep on salt-desert-shrub vegetation in late winter, when the plants are beginning to break dormancy, may be much more damaging than heavy use in early winter when all species are still dormant (Holmgren & Hutchings 1972), as shown in Fig. 3.

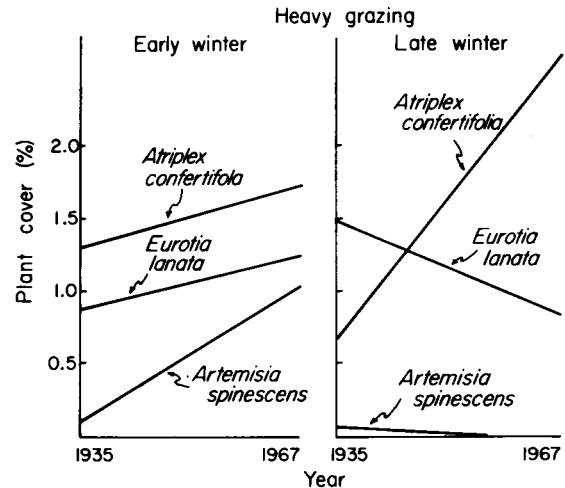


Fig. 3: Vegetation changes under heavy, early and late winter sheep grazing on salt-desert-shrub vegetation in southwestern Utah (after Holmgren & Hutchings 1972). If grazed in early winter, the unpalatable *Atriplex* increases slowly, but the palatable species also increase. If grazed in late winter, *Atriplex* increases markedly to dominate the community, and the palatable species decline to minor status.

Cambios en la vegetación bajo pastoreo intenso por ovinos, temprano y tarde en el invierno, en el desierto arbustivo al suroeste de Utah (de acuerdo a Holmgren & Hutchings 1972). Si el pastoreo se realiza temprano en el invierno la especie no palatable *Atriplex* se incrementa lentamente, pero la especie palatable también se incrementa. Si el pastoreo ocurre tarde en el invierno, *Atriplex* se incrementa marcadamente hasta dominar la comunidad, mientras que la especie palatable declina para ocupar un status inferior.

Sheep prefer herbaceous vegetation when it is active and nutritious. But they will browse the current, annual growth tips of woody vegetation, especially in winter when herbaceous vegetation is dormant and of low nutritional quality. Thus, studies at the U.S. Department of Agriculture's Dubois Sheep Station in southern Idaho at the northeastern edge of the Great Basin have shown that if sheep are grazed in spring and summer in the sagebrush-steppe vegetation, the shrubs will increase at the expense of grasses and forbs. But if the sheep are allowed access to the vegetation only in fall, they will browse the shrubs and convert the vegetation to a grassland (Laycock 1967).

Most of these findings were obtained from long-term studies initiated before the developments in community theory

of the past quarter century and largely proceeded independently of those studies. They were undertaken primarily for heuristic and empirical reasons: to gain some sense of how different grazing treatments affect range vegetation. The failure of range research to maintain close rapport with developments in community theory in the past quarter century probably stems from the fact that those developments have largely been in the area of animal communities.

But in recent years, investigators working on the effects of herbivores on plant communities are beginning to point out the conceptual parallels with animal-community theory (cf. Harper 1969, Lubchenco 1978). It now appears that both plant and animal communities can be viewed in a common conceptual framework in which competition plays a significant role in structuring them.

The individuals of a species are embedded in a matrix of competition with members of the other species in a community. Plants compete with each other for space, soil nutrients, water, and light. Animals compete with each other for food, oxygen, space, and protective habitat. In the absence of disturbance affecting the competitive outcome, the most competitive species prevail in the community and exclude the less competitive ones. The result is a reduction in community diversity. Herbivory is a disturbance which can alter the outcome in plant communities, as predation does in animal communities.

Herbivores tend to be specialized to varying degrees — as Caughley & Lawton (1981) comment "...herbivory is a trade for specialists...". Most herbivores feed on a limited subset of plant species in the community. In the process, the fed-upon species are placed at a competitive disadvantage, and are generally displaced by others not equally fed upon.

What the effects are on plant-community diversity depend on the competitive status of the plant species fed upon, the degree to which the herbivores are specialized, and the number of herbivorous species and their combined range of specializations. As we have seen, single species of highly influential, specialized herbivores like cattle, goats, and deer can profoundly shift vegetation composition.

The generalizations posed by Lubchenco (1978) for intertidal algal communities appear to apply more broadly to the effects of herbivores on other plant communities. If a specialist herbivore concentrates on the uncompetitive plant species, it only hastens dominance by the most competitive and reduces community diversity. But if it feeds on the competitive dominants, it will restrain their exclusion of less competitive species and promote community diversity. In essence, the examples of cattle grazing in grasslands cited above fall in this pattern. With moderate grazing, the dominant decreasers are less abundant, and larger numbers of increasers and invaders enhance plant-community diversity.

The same pattern has been reported for wild herbivores. Bonham & Lerwick (1976) reported higher vegetative diversity in colonies of prairie dogs (*Cynomys ludovicianus*) in the grasslands of eastern Colorado. The rodents fed upon and reduced the abundance of climax, perennial grasses, opening the community to perennial forbs and annuals. Foster & Stubbendieck (1980) observed precisely the same effects of pocket gophers (*Geomys bursarius*) on Nebraska grasslands.

If the herbivores are generalists, the tendency will also be, according to Harper (1969), to promote plant community diversity. My own unpublished research on the effects of black-tailed jackrabbits (*Lepus californicus*), actually a hare, on salt-desert-shrub vegetation in the eastern Great Basin is bearing out this contention. In hare-proof exclosures, the vegetation may succeed to near monotypes of perennial shrubs, depending on the site and soil conditions. But outside the exclosures, where the generalist hares (Westoby 1980, Clark 1981) feed, the vegetation is considerably more diverse. The entire pattern is analogous to the role of predators in animal-community diversity (cf. Connell 1961, Paine 1966, Pianka 1966).

Presumably, the same could be expected from the effects of an aggregate herbivore community. While many of the herbivorous species would be specialized, their collective specialties would constitute a *de facto* super generalist that would prevent a plant community from going to some competitive equilibrium. Given the diversity of herbivores in most vegetation types, perhaps Connell's (1978) genera-

lization that tropical forests and coral reefs do not reach a precise competitive equilibrium could be extended more widely to many vegetations.

The competition and diversity paradigm has obvious practical implications for range management. The succession concept and the studies of cattle effects on grasslands along with the Dyksterhuis and range-condition classifications can be accommodated in this scheme. Succession can be looked upon as the progressive replacement of less competitive forms by more competitive ones. The climax species of "excellent" range conditions are the competitive dominants. In grazing the climax grass species, cattle reduce their competitive abilities which works to the advantage of the competitively inferior increasers. If grazing pressure is then transferred to the latter, they in turn give way to the highly uncompetitive invaders of "poor" range condition.

In the ecotonal and arid areas described above, and depending on which livestock classes are involved, these traditional terminologies may not apply as readily. For example, in the ecotonal types, the balance between species may be tenuous, and dominance may be affected by long-term history of fire or variations in site characteristics. As a result, it may not be entirely clear what the climax species are.

As we have seen, vegetation may be shifted laterally from one type to another depending on whether the most influential herbivore is a grazer or browser. Consequently, what are decreasers and excellent range conditions for cattle may be quite different from what they are for deer or goats. The challenge for the range manager is now to develop an understanding of what combination of plant species provides the maximum desirable production for the particular ungulate (s) he chooses to husband, and what management practices provide that combination over a sustained period.

At earlier developmental stages of the range-management discipline, common use — combined stocking of two or more livestock classes with different forage preferences — was not looked on with favor. The concern seemed to be that if one livestock class could seriously damage a range vegetation, two or more would probably be that much more de-

leterious. But with the newer understandings of vegetation shifts induced by single herbivorous species, common use at proper stocking densities is now viewed favorably as a means of achieving vegetation equilibrium. Colleagues at my own university are experimenting with spring stocking of cattle and horses, both grazers, on winter mule deer range in order to maintain the woody vegetation needed by deer (Smith & Doell 1968, Reiner & Urness 1982).

DISCUSSION

I have now reviewed four aspects of North American research on herbivory, each pursued by largely different groups of investigators operating from different theoretical and applied perspectives. There are, of course, other extensive aspects of the topic which have mostly or entirely been by-passed. For example: (1) The physiological and morphological effects of herbivory on plants. (2) Herbivore nutrition. (3) Except for cycles, the extent to which vegetation is limited by herbivores, and herbivore populations are limited by vegetation, a main theme of Crawley's (1983) book. (4) Herbivory in an ecosystem context: *i.e.* in energy flow and biogeochemical cycling. The space and time limitations of this review did not allow attention to more of these topics.

Any attempt at integrating the four areas that have been discussed immediately encounters contradictions between them that must be reconciled, or knowledge gaps that must be filled, before a synthesis is possible. For example, the general tenor of research on secondary compounds, herbivore-vegetation cycles, and herbivore effects on vegetation composition basically views herbivory as having an exploitive and negative effect on plants — a perspective that contrasts sharply with Owen & Wiegert's (1976) suggestion of mutualism. Any reconciliation of this difference is unlikely without extensive, new research breakthroughs which provide convincing evidence that herbivory improves plant fitness.

If compensation eventually proves to be a widespread phenomenon, it will pose new variables in modeling and managing herbivore-plant systems. If real, it would appear in essence to mitigate the negative effects of herbivores on vegetation, and perhaps

damp cyclic oscillations and shifts in plant-community composition. In its absence, those oscillations and shifts could be expected to be more pronounced. Similarly, the existence of compensation might reduce the pressure of herbivores on plant fitness and lessen the adaptive disparity between short-lived insects and long-lived perennials which Whitham (1983) discusses.

Where, and under what circumstances, do vegetation cycles occur? The examples cited to date seem to involve a single specialized, influential herbivore driving a limited subset of the vegetation, while the remainder of the vegetation seems largely uninvolved. But might the livestock- and deer-induced changes in entire vegetations that we have discussed represent short segments of what might be long-term cycles, stable or damped, if allowed to run their course? This prospect does not appear to have been given serious attention by the range-management profession.

Might cyclic vegetation changes be prevented by a spectrum of specialist herbivores, or by a complex of generalists, which feed over the entire vegetation? I have suggested (Wagner 1981) that predator-prey cycles occur in relatively simple systems in which the major predator has few or no alternate prey, and the major prey species is fed upon largely or only by the major predator. Addition of alternate prey and predator species tends to dissipate the Lotka-Volterra dependency inherent in two-species systems and damp out the oscillations. Might the same principles apply in herbivore-vegetation cycles? And might this contradict the prevailing view of recent years that there is no positive link between stability and complexity?

These are the kinds of questions that should guide research and theoretical inquiry in order to bring the four somewhat disparate areas of herbivory research toward a coherent theoretical framework.

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