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INFLUENCE OF GRAZING ON PLANT SUCCESSION OF RANGELANDS

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INTRODUCTION

In considering succession in this review, we are concerned with secondary, not primary, succession. We are concerned with changes of plant cover on a soil that has already been formed, not with the action and interaction of organisms and environment over the ages, by which a soil is built out of raw rock. Secondary succession is what man must manipulate if he is to "manage" the range resource: primary succession is not something he can manage in any practical sense because his life span is too short. If his management is successful, by definition the phases of primary succession involved in normal soil development can go forward, presumably as they went forward in a state of nature. When his management is unsuccessful, he may set destructive processes in motion by which soils built over thousands of years can be wiped out in a few decades.

In speaking of range we are considering not only extensive native grasslands but also more diversified plant communities where the native vegetation is useful for grazing of either wild or domestic animals. In the western United States, these ranges may be dominated by forbs, grasses and sedges at high elevations; by aspen or conifer forests at intermediate elevations; by mixtures of shrubs and herbs in the foothills and better-watered plains; and by desert shrubs in the most arid environments. The term "range" in contrast to "pasture" refers to lands clothed mostly with native vegetation that cannot be grazed heavily with safety, where the principal management tool is manipulation of the grazing animal to achieve desired successional trends. Intensively managed pasture, where introduced species are dominant, where grazing is relatively heavy and where improvement is brought about by such agronomic practices as artificial fertilization, seeding and irrigating, is therefore excluded from consideration here.

To many people, perhaps to most, the range is simply a romantic setting for stories about the Old West—a carefree land where men were (once) men. The range is not something just of the past, however; it is still with us, not so much a setting for heroics as a resource of considerable economic importance. Roughly about three-fourths of the area of the United States west of the hundredth meridian is considered to be livestock range (U.S. Forest Service, 1936) and even more is wildlife habitat. On the western range, there are estimated to be some nine million range cattle, nine and one-half million domestic sheep, and four million big-game animals (Wasser *et al.,* 1957).

Most of this vast area has been so heavily grazed for so long that the original plant cover has been depleted, and in many places destroyed. Although unregulated livestock overgrazing is the principal cause, the effects of overgrazing by big game have become increasingly apparent in recent years. Deer, elk and moose have increased in number to such a degree that in many places they are destroying their own habitat.

The economic and ethical consequences of range mismanagement go far beyond damage to the forage resource. There is very little of the western range where, because of depletion of the plant cover by overgrazing, accelerated erosion has not destroyed a portion of the soil mantle and thus reduced the productivity of the site. The fact that the western tributaries of the Mississippi, as well as those of the Colorado and Columbia, flow through rangelands during most of their course has much to do with the load of sediment they carry. Vast expenditures of public funds have been made, and more are planned, for storage reservoirs along these river systems, but the useful life of these reservoirs is being unnecessarily shortened by accelerated siltation (Cooke *et al.,* 1950). It was estimated a generation ago that three-quarters of the 729 million acres of western range were contributing materially to the siltation of streams (U.S. Forest Service, 1936). Possibly improved grazing practices have lessened the rate of siltation somewhat, but if a survey were to be made today, more adequate recognition of range depletion and what constitutes accelerated erosion would probably show that the figures of the mid-thirties are still reasonably applicable.

Although the western range may still be regarded in more civilized parts of the world as wasteland, and admittedly its acre values for forage are generally low, the vastness of its area makes it important in the national economy. Much of this area is too difficult of access or too low in productivity to warrant intensive pastoral practices, so that improvement of its protective plant cover and forage value must be achieved extensively—that is, by natural successional processes. Ecological understanding of these processes, which must form the basis for effective management, is therefore imperative. The achievement of such understanding is a scientific challenge of the first order.

OBJECTIVES

That overgrazing depletes the range is true by definition. The process has been described succinctly by Weaver and Clements (1938) as follows:

> "The more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competition to the side of the latter. Because of more water and light, their growth is greatly increased. They are enabled to store more food in their propagative organs as well as to produce more seed. The grazed species are correspondingly handicapped in all these respects by the increase of the less palatable species, and the grasses are further weakened by trampling as stock wanders about in search of food. Soon bare spots appear that are colonized by weeds or weedlike species. The weeds reproduce vigorously and sooner or later come to occupy most of the space between the fragments of the original vegetation. Before this condition is reached, usually the stock are forced to eat the less palatable species, and these begin to yield to the competition of annuals. If grazing is sufficiently severe, these, too, may disappear unless they are woody, wholly unpalatable, or protected by spines".

So much for overgrazing; but what of grazing? Grazing animals must certainly be reckoned an elementary environmental factor in the ecology of most of the world's herblands. If the logic of selective grazing be followed out, the existence of any grazing pressure means a handicap to some desirable species or group of species, and thus by successive stages, a descending spiral of depletion. But pristine herblands were not depleted. Evidently they stood up very well to grazing, even though at some times and places the grazing pressures of wild herds were marked (Larson, 1940). If the pictures of pristine herbland pieced together by ecologists are correct, its outstanding characteristics were a near-maximum of cover for the site and a great variety and high proportion of palatable species. Obviously grazing—as opposed to overgrazing—did not have this depleting effect.

Furthermore, we have the observed fact of range improvement under grazing to consider, i.e., improvement in the face of grazing pressure. If the mechanics of palatability were adequate to explain all successional trends on the range, grazing, by handicapping the more palatable plants and encouraging the less palatable ones, should not permit improvement to occur. But improvement under grazing does occur, apparently about as fast, sometimes, as improvement under no grazing at all. How are such trends possible? Does grazing benefit the vegetation in some way that counteracts its harmful effects?

Such questions as these prompt this review. Unfortunately the literature of range ecology does not have much to offer in the way of answers: the word "grazing" in many titles should properly be "overgrazing". This preoccupation with the unnatural and extreme is understandable because overgrazing has been so common; but it does make difficult an evaluation, from published evidence, of grazing as a natural ecological factor. Of this, however, not much is known.

For one thing, degrees of grazing are not easily defined. The range that will support a given number of animal months during one period of years may be capable of supporting twice as many during a wetter period or perhaps only a third as many during a drier period. A depleted range may be heavily utilized by the same number of animals that would make only light use of the same range in good condition. The terms "lightly", "moderately" and "heavily" grazed are not only restricted in significance by being relative instead of absolute, but, unless production of forage and numbers of animals are specified, they are highly subjective. What one author means by "light" grazing may very well be "moderate" or even "heavy" grazing to someone else. This has been particularly observable with the passage of time. The judgments of early students of range ecology were influenced not only by grazing experience with pastures in more humid environments but also by the fact that much of the range was in poor condition and that overgrazing was customary. At a time when little was known about requirements of the plants or protection needs of the site, much closer utilization was considered moderate than is considered moderate today.

For another thing, difficulties of measuring range vegetation precisely have encouraged the study of extremes. Many studies contrast heavy grazing with no grazing, but few evaluate the effects of light grazing against no grazing. Most studies are short-term rather than long-term, and naturally the trends set up under heavy grazing are the soonest observed. Some of the difficulties of measuring range vegetation arise from the fact that most grazing types contain numerous species of divers growth forms, of which few react exactly alike. Trends develop, too, as a result of the interactions between plants and weather, insects and rodents as well as of the grazing treatments that are being studied. Hence, the critical student is obliged to regard the significance of small differences—the sort of differences one might expect between light grazing and no grazing—with skepticism.

In this review we shall examine successional trends by the major plant types of the United States, beginning with the true prairie of the Great Plains and moving westward. Most of the changes resulting from severe grazing, we shall see, conform to the pattern outlined in the above quotation from Weaver and Clements. However, rather than dwell on the destructiveness of overgrazing, which would be to belabor the obvious, we shall emphasize studies that seek to evaluate the effects of light or moderate grazing. From this perhaps we can build a picture of the ecological influence on plant composition of grazing as it might be practiced, and particularly of any constructive influence that light or moderate grazing may exert. Then we shall examine successively the effects of herbage removal on the individual plant and on the environment, still with the objective of learning to what extent grazing can be considered a constructive ecological force.

CRITERIA

The fact that there are many technical difficulties in measurement of vegetation is recognized by everyone who has tried to compare responses in two parts of any plant community that includes a diversity of growth forms. Even more fundamental than the problem of getting methods adequate to distinguish the differences one desires to measure is the problem of standards by which to evaluate the differences. Obviously a treatment that results in death of the plant or its diminution in the stand can be considered harmful to that plant. From the standpoint of successional development, of course, the loss of the plant may be an advantage. This example illustrates the fact that, whether we wish it or not, subjective judgments must be included in evaluations of changes that take place—up or down the successional scale, good or bad, from the standpoint of some phase of land management.

Ordinarily we shall suppose that a treatment which results in augmenting the production of herbage of a species is advantageous to that species. This need not always be so. For example, clipping a shrub may stimulate its vegetative growth but depress its reproductive growth. How does one equate such very different things?

We shall assume that the best integrated measure of the abundance or volume of vegetation is given by weight production. Other measures—cover, basal area, number, frequency of occurrence—are only approximations of total weight and in many instances may bear a contradictory, not a direct, relation to it. Cover, perhaps the most generally used measure, is here considered next in value to weight, but even cover may be misleading. For example, in successional trend from depleted range to some level closer to climax, tall species replace short ones, weight production increases, and cover, which is at a maximum with a turf or mat growth form, declines. The inadequacy of cover for some purposes is strikingly illustrated by a quotation from Albertson *et al.* (1957) in which change in short-grass cover is referred to: "This decrease was presumed to be due to drought, although in some cases, particularly in ungrazed areas, it was due, in part, to accumulated mulch." Here two very different causes, drought and mulch, which probably had opposite physiological effects on the plants, gave rise to a similar response when the amount of vegetation was evaluated in terms of cover.

The reviewer will be the first to concede that he has not done an adequate job of evaluating the significance of results as they may be affected by the methods used. The variations that necessarily occur because of difference in method, which themselves arise partly because of the complexity of vegetation, make a complex subject no simpler.

TRUE PRAIRIE

The main features of true and tall-grass prairies (which are here considered together) have been outlined by Weaver and Clements (1938). Much of the area of this former grassland is now under cultivation, and most of that which is unbroken by the plow has been greatly altered as a result of heavy grazing. Dr. J. E. Weaver and his students at the University of Nebraska have done much to elucidate the character of the true and mixed-grass prairies and the changes they have undergone because of overgrazing and drought.

The line dividing true prairie from mixed-grass prairie to the west has been described as an ecotone about 50 miles wide through eastern Nebraska and central Kansas at approximately 98° 30′ W. longitude (Weaver and Bruner, 1954). During the great drought of the mid-thirties this line was shifted eastward, and true prairie was replaced by mixed-grass prairie in an area 100 to 150 miles wide in central Kansas, eastern Nebraska and eastern South Dakota.

Weaver and Hansen (1941a) describe the process of degeneration under grazing in eastern Nebraska. Those species that decrease in abundance under grazing ("decreasers") include ten grasses and 45 forbs, of which 13 are legumes. These species were major dominants of the prairie in its virgin state. Some of them are: *Andropogon gerardi, A. scoparius, Sorghastrum nutans, Panicum virgatum, Stipa spartea, Amorpha canescens,* Petalostemon spp., Psoralea spp., Aster spp., and Liatris spp. Those species that increase under grazing pressure ("increasers") include ten grasses and 28 forbs. Some of these are: *Poa pratensis, Agropyron smithii,* Bouteloua spp., *Buchloe dactyloides, Carex pennsylvanica, Achillea occidentalis, Antennaria campestris, Artemisia gnaphalodes,* Solidago spp., and Vernonia spp. "Invaders", species that come into the stand when grazing is so severe as to handicap the increasers, include many annuals and unpalatable plants. Some common genera are: Bromus, Eragrostis, Hordeum, Schedonnardus, Sporobolus, Ambrosia, Cirsium, Euphorbia, Plantago, and Verbena.

Weaver and Hansen describe five degrees of condition, the highest approaching the climax and the lowest dominated by short grasses and weeds, with evidence of soil erosion. They do not relate range condition to damage from drought; apparently drought overrode differences in plant composition. The degree of grazing during and after drought, however, had a very marked influence on recovery.

In the same locality Darland and Weaver (1945), Weaver and Darland (1948) and Voigt and Weaver (1951) describe the process of degeneration in specific areas. In the last-named study, a diagram, patterned on one prepared by Dyksterhuis (1949), shows the proportions of decreasers, increasers and invaders in four condition classes and an extrapolation to their presumed proportions in the climax, from which we derive the following percentages:

	Climax (extrapolated)	Excellent	Good	Fair	Poor
Decreasers	82	67	34	4	2 or less
Increasers	16	30	61	88	32 or less
Invaders	2	2	3	6	47 or more
Forbs (interpolated)	?	1	2	2	19
	100	100	100	100	100

Note that the "excellent" class is regarded as being somewhat altered from the original climax grassland. The authors concede that the proportion of forbs may be unduly low in the "excellent" class because of grazing and drought.

Weaver and Tomanek (1951) classify condition on a 290-acre range in the same locality and characterize each condition class. Essentially the same pattern emerges as from other studies. It is interesting that the average of samples from the "excellent" class comes fairly close to the extrapolated "climax" from Voight and Weaver's study, with 81 percent of the basal area decreasers, 18 percent increasers, and one percent invaders. Probably too much significance can be attached to such similarities, for the proportions in the different classes may be expected to vary with differences in site, weather and other environmental influences besides grazing, not to mention differences between ecologists! The proportions in the good, fair and poor classes diagrammed by Dyksterhuis (1949), for example, are very different from those diagrammed by Voight and Weaver (1951).

Dry weight and depth of roots in prairies decrease with intensity of grazing and decline in range condition (Weaver and Darland, 1948; Weaver, 1950). The differences are caused partly by reduced vigor of the tall and mid-grass decreasers, and partly by invasion of the shorter rooted *Poa pratensis* and short grasses, with increased grazing pressure.

In the sand hills of northern Nebraska, Tolstead (1942) recognizes three stages in degeneration under grazing. When the most palatable tall grasses, *Andropogon hallii, Eragrostis trichodes* and *Panicum virgatum,* are grazed out, *Calamovilfa longifolia* and *Sporobolus cryptandrus* become dominant. Under more severe grazing pressure these decline, and *Muhlenbergia pungens* and certain weedy forbs become dominant.

In contrast to the preceding type of approach, in which the process of degradation is described, Weaver and Hansen (1941b) describe regeneration over a four-year period near Lincoln. They compare a native pasture under four years of protection from grazing with native prairie that had not been grazed but had been mowed annually. Although the pasture "had apparently never been greatly overgrazed", its composition was quite unlike that of the prairie. During the four-year period of protection there was a gradual replacement of pasture grasses, principally *Poa pratensis* and *Sporobolus cryptandrus,* with prairie grasses, chiefly the Andropogons and *Bouteloua curtipendula.* From a follow-up study (Weaver, 1954) it appeared that, 13 years after the drought, the former pasture had neither the richness of flora nor the intimate intermixture of species found in the mowed prairie. The influence of mowing in modifying climax prairie, incidentally, is suggested by an observed thinning of *Poa pratensis* as a result of but one year's accumulation of mulch. Presumably *P. pratensis* could not long survive among the taller species in unmown true prairie.

In central Missouri Drew (1947) concluded that mowing modified tall-grass prairie, mainly by reducing certain forbs, and that a distinction must be made between "domesticated" prairie and the original native grassland. The mowed pasture of Drew's study was then divided by a fence and for 11 years one-half was grazed heavily by cattle (Kucera, 1956). The cover of tall and midgrasses was greatly reduced under grazing, as compared with mowing, and there was a great increase of "invaders". One notable effect of heavy grazing was the reduction in total number of species from 115 to 67.

Launchbaugh (1955) compared fields in the San Antonio Prairie that were used only for hay, were used for hay and grazed, or were grazed at different intensities. These comparisons enabled him to draw up a pattern of decreasers, increasers and invaders. Unlike Drew, Launchbaugh concluded that areas subjected only to annual mowing adequately represented climax vegetation, basing his conclusion on the fact that certain perennial forbs appeared to be able to recover from mowing and complete their life cycle each year. Although hay yields from the grazed meadows were considerably reduced, moderate grazing of hay meadows did not alter the plant composition greatly from that of ungrazed hay meadows that were mowed.

A little to the west in a somewhat drier environment on the Edwards Plateau, Buechner (1944) set up six stages of succession based on degree of depletion from overgrazing. The highest stage is dominated by *A. scoparius* and *Stipa leucotricha;* the lowest is bare ground. Notable in the intermediate stages of Buechner's scheme are several perennial species of Aristida. Buechner has reason to believe that a stage dominated by Aristida spp. is lower successionally than stages dominated by Bouteloua spp. and Buchloë—a departure from the usual ranking of short and midgrasses. Buechner (1950), in studying the pronghorn antelope, also outlined a successional series in four stages in southwestern Texas. The climax is characterized by Andropogons, *Bouteloua curtipendula* and numerous forbs, including several species of Dalea, *Desmanthus cooleyi* and *Gaura coccinea*—all choice antelope food. Intermediate stages are characterized by species of Bouteloua and Aristida, and the lowest stage by *Triodia pilosa, T. pulchella* and *Aristida divaricata.*

On the Fort Worth Prairie, Dyksterhuis (1946) compared plant composition on heavily grazed range, carefully managed range, and relic areas that had had little or no grazing. From a comparison of indices derived by multiplying coverage by frequency, he concluded that the principal decreasers were *Andropogon scoparius, A. gerardi, Bouteloua curtipendula, B. hirsuta* and *Sorghastrum nutans,* and that the principal increasers were *Stipa leucotricha,* Aristida spp., *Buchloë dactyloides* and *Triodia pilosa.* Like Launchbaugh (1955), Dyksterhuis found *Andropogon saccharoides* to be more abundant under some protection than on either overgrazed range or in relic areas of climax grassland. This was also true of *Sporobolus asper.*

Immediately to the west, in the Western Cross Timbers of Texas, Dyksterhuis (1948) showed the usual decrease of tall grasses and midgrasses under heavy grazing, and increases of short grasses, annuals and woody species. He attributed extension of oak forest or woodland to reduced competition for soil moisture by herbaceous vegetation and to reduced frequency of fires, both because of overgrazing. This treatment includes a discussion of the phenology, gross morphology and seasonal variations in palatability of the important species. The major dominant of the pristine vegetation, *Andropogon scoparius,* for example, is eagerly grazed by cattle every month of the year. During September, even on lightly grazed range, cattle feed exclusively upon the exserted, immature inflorescences of *A. scoparius,* so that virtually the entire seed crop is consumed. The upright habit of this plant and its long season of palatability make it especially susceptible to damage by grazing.

In central Oklahoma Kelting (1954) compared a moderately grazed portion of a 1,000-acre pasture with a five-acre area that had not been burned or grazed for 25 years, although it had been mowed for hay nine years before the study. Cover was greater on the grazed than on the relic area. *Andropogon scoparius* made up approximately half the cover on the grazed pasture, but only from a tenth to a quarter of the cover on the relic prairie; on this site it would appear that some tall grasses, which were more abundant on the relic area, had been reduced by grazing, so that the midgrass, *A. scoparius*, was favored. Such a trend is also shown by Drew's (1947) data from tall-grass prairie in Missouri. On Kelting's moderately grazed pasture most of the plants of *A. scoparius* were left untouched, whereas patches between them were grazed closely, thereby allowing some of the shorter grasses and forbs to become established. The larger number of species on the grazed pasture—64 as compared with 36 on the relic area—is attributed to the disturbance of grazing. Kelting concluded from this single-season study that moderate grazing increases the amount of forage because cover percentages and oven-dry weights of living material were greater in the grazed pasture than in the virgin prairie. He reported still higher yields from a nearby pasture that had not been grazed since the middle of the previous growing season. Perhaps as a consequence of greater herbage production, organic carbon was considerably greater in the pasture soil than in the prairie soil, even though the mulch cover was less.

In the same general area in Oklahoma, although referred to as mixed-grass prairie, Smith (1940a) showed the usual decreasers and some increasers (*Panicum scribnerianum, Bouteloua curtipendula*) to decrease in abundance, even under an intensity of grazing classified by him as "moderate". Gernert (1936) clipped plots of native prairie with a hand sickle and found a tendency over six years for yields to be greatest on plots clipped two, three and five times per year, and least on plots clipped eight, nine and ten times. Root weights and volumes tended to follow the same pattern.

In the Flint Hills of Kansas Aldous (1930) found that yield of vegetation varied inversely with frequency of clipping. Under the most severe treatments the Andropogons decreased, and weeds and *Bouteloua hirsuta* increased. To indicate how severe the heavy clipping treatments in this study were, Anderson (1940) pointed out that they accomplished in three seasons what had taken 40 years or more of season-long grazing to do. By deferring spring grazing until mid-June, instead of beginning grazing in mid-April or early May, Anderson showed that *Andropogon gerardi* decreased to about the same extent under both systems, *A. scoparius* decreased much less under deferred than under continuous grazing, and *Bouteloua curtipendula,* which increased under both systems, increased much more under deferred grazing. *Sporobolus cryptandrus* and *Buchloë dactyloides* increased greatly under continuous grazing and changed relatively little under deferred grazing. Thus continuous grazing had essentially the same effect as heavy grazing in other experiments: it decreased midgrasses and encouraged short grasses and relatively unpalatable species.

MIXED-GRASS PRAIRIE

In mixed-grass prairie, which intergrades with true prairie, a similar pattern of increasers, decreasers and invaders has been found (Brinegar and Keim, 1942; Allred, 1945; Branson and Weaver, 1953).

Tomanek and Albertson (1953) compared three areas near Hays, Kansas: "One pasture had been stocked very heavily, one moderately, and a third had never been more than lightly used since the days of the buffalo". As might be expected, tall grasses and midgrasses made up most of the vegetation on the lightly grazed range and least on the heavily grazed range, with the proportions of short grasses in reverse order. Reactions of species varied somewhat from site to site. *Bouteloua curtipendula* "reacted like both a decreaser and an increaser. On the hillsides and ridges it became more abundant with moderate use, but as the pressure became greater it decreased. On the rocky breaks, however, it increased steadily with greater utilization". It would appear that the pattern of increasers, decreasers and invaders, while generally valid on the Plains, becomes complicated in application to vegetation of broken topography.

Similar results were obtained by Tomanek and Albertson (1957) in western Kansas. *Bouteloua curtipendula* again reacted variously with site, and *B. gracilis* departed from the increaser role assigned to it in a more humid environment. It increased with moderate grazing but decreased under heavy grazing on most sites, and on one it decreased under moderate as well as heavy grazing. Total yields tended to decline with intenstiy of use during both years of study. These were mainly the resultant of declining yields of midgrasses and increasing yields of short grasses; and the yields of total forbs, which followed no set pattern, tended to complicate the trend.

Probably the two most important factors affecting range productivity are available soil moisture and intensity of grazing. The recovery of range vegetation following the great drought of the 1930's in relation to grazing intensity is therefore a subject of considerable interest; since the influence of drought has been more thoroughly studied on mixed-grass prairie than on any other type of vegetation, we shall consider it here.

In evaluating the results of drought studies, it must be kept in mind that the distinction between living and dead vegetation is uncertain during periods of extreme drought. Statistics on degree of mortality must therefore be regarded with healthy skepticism, and differences, to be regarded as significant, should properly be supported by observations of survival after the recurrence of normal weather.

In 1935 Savage (1937) studied survival of Plains grasses in terms of basal cover from the Panhandle of Texas to central Nebraska. He concluded that, for a given degree of drought, survival was better on ungrazed than on moderately grazed range. Where *Buchloë dactyloides* was a dominant part of the cover in localities where the drought was least severe, however, total grass cover increased with grazing intensity. This latter conclusion was supported by clipping studies. Other authors (e.g., Albertson and Weaver, 1944) have recorded a phenomenal increase in Buchloë as one of the striking effects observed during recovery from drought.

Weaver and Albertson (1936) agree with Savage in showing a greater increase in short-grass cover near Hays, Kansas, between 1932 and 1935 under moderate grazing than under no grazing, and, surprisingly, they also show a 20-percent drought loss in basal cover in an ungrazed *Andropogon scoparius* type as compared with an 8½-percent loss under moderate grazing. This observation is supported by comparisons in three localities where more loss of *A. scoparius* occurred between 1934 and 1935 on ungrazed than on moderately grazed range.

The authors explain that lightly or moderately grazed vegetation uses less water than the denser vegetation of ungrazed prairie and so maintains a greater basal cover. They did not study soil moisture under different degrees of use, however; so there is no objective support for this inference. Practically nothing is known about the effects of light or moderate grazing on roots in the field, but in view of the fact that light clipping does not appear to enhance root growth (Crider, 1955) and that heavy grazing has been shown to decrease penetration of roots (e.g., Tomanek and Albertson, 1957), the validity of this explanation is doubtful. Costello and Turner (1941), who observed five moderately grazed areas in the short-grass type in which cover was greater than on adjacent protected areas, also explained the difference by what we may call the "suicide hypothesis", but they likewise offer no soil-moisture observations or other evidence to support it.

Perhaps it is pertinent to note at this point that differences in degree of cover (or "density") are not necessarily paralleled by differences in area of transpiring surface.

Weaver and Albertson (1944) present changes in basal cover over a longer period, from 1932 to 1943, also in the short-grass type near Hays, Kansas. In contrast to their earlier data, up until 1938 these show the ungrazed range to support most cover, the moderately grazed range an intermediate amount, and the overgrazed range the least. Between 1939 and 1943, years of rapid recovery from drought, these consistent relations did not hold, however, and the same explanation is again invoked, unsupported by soil-moisture measurements, that the ungrazed vegetation used the most soil water. This report also shows a graph of recovery of basal cover between 1935 and 1943 in an *Andropogon scoparius* type in which ungrazed and overgrazed vegetation recovered at about the same rate. This is explainable because of the greater cover of short grass, particularly Buchloë, on the overgrazed range.

Short-term studies in western Kansas (Cressler, 1942; Lacey, 1942; Tomanek, 1948) suggest that mixed-grass range is more productive of cover, or recovers from drought and dusting more rapidly, under light or moderate grazing than under no grazing. Despite absence of statistical control in these studies, the conclusion is probably valid: some grazing in the mixed-grass type favors short grasses at the expense of midgrasses and results in an increase in cover. Furthermore, production of herbage in terms of weight may be stimulated for a year or two (Albertson *et al.,* 1953).

In the mixed-grass association in western Kansas, Albertson and Weaver (1944) selected pastures in four degrees of condition that had been reduced to short grass by drought and overgrazing, and studied them through two years of recovery, 1940 and 1941. As might be expected, they found that basal cover and yield tended to decline from the best to the poorest degree of condition. Utilizing four clipping treatments, these authors clipped the grass to one-half inch monthly (May through August) and to ground level at the end of the season as follows:

Treatment 1: Clipped monthly in 1940 and 1941.
Treatment 2: Clipped monthly in 1940 and at end of 1941.
Treatment 3: Unclipped in 1940; clipped monthly in 1941.
Treatment 4: Unclipped in 1940; clipped at end of 1941.

In all but the poorest pastures the 1941 yields of short grasses followed the order: $4 > 3 > 2 > 1$. Response of grasses in the poorest pastures was erratic, presumably because these pastures contained large numbers of annual weeds. Thus production, even of short grasses, varied inversely with intensity of utilization, but if midgrasses had been abundant, it seems probable that the reaction of the short grasses might have been different.

Albertson *et al.* (1957) evaluated the 1952-55 drought in the central Great Plains in relation to grazing. They estimated predrought cover and live cover ("density") in 1955, and calculated from these estimates the degree of loss due to drought and grazing. The heavily grazed ranges lost a greater proportion of their predrought cover than the moderately grazed ranges, and these in turn less than the ungrazed ranges. It would thus appear that, even by the criterion of cover, moderate grazing did not help the vegetation withstand the influence of drought.

Albertson *et al.* (1953) conducted a six-year clipping study in a short-grass type near Hays, Kansas, which is particularly interesting because some of the treatments correspond to light or moderate grazing. From the authors' summary histogram of the six-year average yield of clipped and unclipped grass, one may estimate that the lightest two treatments removed between 20 and 25 percent of the total production. They found, as most studies show, an inverse relation between frequency or intensity of clipping and yield. This became obvious only after the third and fourth years, however, because clipping stimulated production during the early years. In the last two years of the study total production declined in the following sequence of the three lightest treatments:

Unclipped.

Beginning June 25 clipped every six weeks at a height of two inches on 60 percent of the area; remainder of the area unclipped.

Beginning June 10 clipped every four weeks at a height of one and one-half inches on 80 percent of the area.

At the end of the study the number of weeds was less on the unclipped than on the clipped quadrats, and broad-leaved forbs were particularly numerous on the severely clipped quadrats.

Another clipping study that includes some light treatments is one by Whitman and Helgeson (1946) in southwestern North Dakota. In this study total grass yields declined over a seven-year period under all intensities of clipping, even clipping only once in a season to a height of three inches. This intensity is estimated by the reviewer to represent 20-percent removal of *Bouteloua gracilis,* 25 percent for *Carex filifolia,* 43 percent for *Stipa comata,* and 73 percent for *Agropyron smithii.* These estimates are considered by Whitman (personal communication) to be close to correct. On one of the two sites forbs increased to compensate for the loss in grass, but, since forbs increased inside the exclosure generally, not just on the clipped plots, this increase may have been caused by some factor other than clipping.

Numerous studies on the Plains show the disadvantage to plants of severe grazing or clipping or that the short grasses are favored by clipping or grazing in proportion to the degree to which the taller growing midgrasses are handicapped (Sarvis, 1923, 1941; Black *et al.,* 1937; Lang and Barnes, 1942; Clarke *et al.,* 1943; Holscher, 1945; Lodge, 1954).

Sarvis (1941) concluded at Mandan, North Dakota, that deferred and rotation grazing would permit closer utilization than the vegetation could tolerate under continuous grazing. Rogler (1951), reporting on a continuation of these same experiments until 1946 (they had begun in 1916), concluded that no major changes in plant composition were caused by moderate continuous grazing (1 steer to 7 acres from mid-May to mid-October), or by a somewhat heavier degree of rotational grazing (1 steer to 5 acres). Under these intensities of use, decreasers (*Agropyron smithii, Stipa comata, Koeleria cristata, Psoralea argophylla*) were still abundant after 34 years, and increasers (*Artemisia frigida, Bouteloua gracilis*) either decreased or were maintained at about the same level. The emphasis by these authors and by Black *et al.* (1937), who could detect little or no injury to the vegetation at Ardmore, South Dakota, by close grazing or clipping, is upon animal weights; and their analysis of the vegetation from the standpoint of our inquiry suggests only that short-grass vegetation of the northern Great Plains is remarkably resistant to grazing.

Hanson *et al.* (1931), studying spring-deferred and continuous systems of grazing at the western edge of the Plains in Colorado, showed that *Agropyron smithii* was encouraged by deferred and rotation grazing, and that *Bouteloua gracilis* tended to be most abundant under continuous grazing. Differences in vegetation were not so marked as to indicate a very heavy degree of grazing under either system. The authors concluded that increasing abundance of *Psoralea tenuiflora,* *Artemisia gnaphalodes* and *Sophora sericea,* and decreasing abundance of *Senecio perplexus, Helianthus pumilus* and *Astragalus drummondii* may be used as delicate indicators of downward range trend.

Comparing small relic areas, such as cemeteries, with heavily grazed range in eastern Montana, Wright and Wright (1948) showed that dominance by short grasses and midgrasses had given way to dominance by the unpalatable shrubs, *Artemisia tridentata, Chrysothamnus nauseosus* and *Gutierrezia sarothrae,* under heavy grazing.

Larson and Whitman (1942) present a comparison in southwestern South Dakota that is especially interesting because the harvesting treatments do not appear to have been severe. They compare six-acre Medicine Butte, which apparently had never been grazed even by wild animals, 79-acre Little Wolf Table, which had had moderate intermittent use since settlement, and 600-acre Big Wolf Table, which had been mowed and grazed lightly for 40 years. Data on frequency, abundance and production show that there is a trend from midgrass to short-grass dominance with increasing use, and a marked, parallel trend in the amounts of accumulated litter. Any degree of use would therefore appear to handicap the midgrasses in favor of the short grasses. This study supports Larson's (1940) suggestion that there were enough buffalo and other wild animals on the Plains to maintain the short-grass climax before the advent of domestic livestock.

On the basis of soil and relic areas, Moss and Campbell (1947) have outlined the pristine extent of a northern prairie dominated by *Festuca scabrella* in northern and western Alberta, and its contact with the mixed-grass prairie dominated by *Stipa comata* in the southeastern third of the Province. These authors believe that the original Festuca association included about 20 grass, three sedge, ten shrub and 115 forb species, most of which were rare or occasional. Somewhat more than 100 additional species also occur in the grassland but are considered more characteristic of other communities. The effect of grazing and mowing has been to reduce Festuca and increase other species, with Festuca tending to persist in moist situations and in the protection of shrubs. Shrubs and such forbs as *Lupinus leucopsis* and Artemisia spp. become abundant under grazing but are kept down by mowing. In some areas *Carex eleocharis* becomes dominant under grazing; elsewhere Carex spp., *Artemisia frigida* and Antennaria spp. dominate, together with *Stipa comata, Bouteloua gracilis* and *Agropyron smithii.* It is believed that these latter species, characteristic in mixed-grass prairie farther south, persisted on dry, south-facing slopes or certain kinds of soils, and have spread to overgrazed pastures since settlement. *Andropogon scoparius* is noted as having this same characteristic in southwestern Alberta. Moss and Campbell point out that certain woody plants invade this grassland, notably willows and poplars, followed by conifers, and that the invasion is retarded by grazing. This is in contrast to invasion of grassland by woody plants in drier areas, a process that appears to be strongly encouraged by grazing.

DESERT GRASSLAND

Jardine and Forsling (1922) outlined the course of deterioration as a result of overgrazing *Bouteloua eriopoda* on the Jornada Experimental Range near Las Cruces, New Mexico. According to this account, the first stage is marked by an abundance of annual grasses and forbs and short-lived perennials scattered among the Bouteloua. This is followed by dominance of certain perennial grasses and forbs, including species of Sporobolus, Croton, Solanum and Psilostrophe, and this stage is followed by dominance of the half shrub, *Gutierrezia sarothrae.* The final stage of deterioration, accompanied by the effects of wind erosion, is dominance by *Prosopis glandulosa.* In the same area during a three-year period of ample rainfall and lessened grazing, Campbell (1929) outlined a reverse course of succession from *P. glandulosa* sand dunes to the *B. eriopoda* climax in a somewhat different sequence: mat forbs, ruderal weeds, Gutierrezia, Sporobolus and other grasses, and finally *B. eriopoda.* There is a suggestion, in a six-year study of trends in Bouteloua and Gutierrezia (Campbell and Bomberger, 1934), that Gutierrezia is the less stable because of susceptibility to drought and insects. Also, as Bouteloua increased, forbs, annual grasses and the perennial grasses, *Sporobolus flexuosus, Aristida pansa* and *A. purpurea,* declined. These observations, and fenceline comparisons made by Gardner (1951), lend support to some of the intermediate sequences of successions previously deduced. Gardner concluded that an increase in unpalatable half shrubs such as Gutierrezia marked an early stage in recovery of former desert grasslands now dominated by shrubs like *Larrea divaricata.* No evidence is given in any of these papers of observed replacement of long-lived shrubs, such as Prosopis or Larrea, by herbaceous plants.

The effects of grazing *B. eriopoda* on the Jornada Experimental Range have been reported by Nelson (1934) from 1915 to 1927 and by Paulsen (1956) through 1953. With one interesting exception, changes of grass cover varied inversely with grazing intensity. The exception was the maintenance of more cover under conservative grazing (less than 40 percent utilization) than under complete protection. The explanation suggested (Nelson, p. 31) is that "conservative grazing appears to break up the large, separated tufts formed under freedom from use into smaller tufts better adapted to make efficient use of the available soil moisture." Why this process should be an improvement in its physiological effect over the breaking up of ungrazed tufts because of drought (Nelson, p. 17) is not clear. As with previously noted explanations of this sort, no evaluation of actual soil moisture was made.

In southern Arizona, Canfield (1948) found that tall, coarse-stemmed grasses, such as *Trichachne californica, Bouteloua curtipendula* and *B. eriopoda,* which were scarce on heavily grazed range, made up a high percentage of the composition after long periods of protection. Overgrazing caused a tendency toward dominance by such short-lived perennial grasses as *Bouteloua rothrockii* and *B. filiformis,* and by such shrubs as *Aplopappus tenuisectus* and *Prosopis velutina.* Canfield concluded that, when the soil had not been greatly eroded and the composition of the vegetation not drastically altered by overgrazing, the rate of range recovery under conservative grazing is approximately equal to that under total protection.

Comparative data given by Canfield, be it noted, are in terms of percentage composition, not in terms of cover or yield. In comparing a grazed site with one that had been protected for 30 years near Silver City, New Mexico, Gardner (1950) found little difference in percentage composition, but about half as much basal area of grasses as on the protected range.

Numerous students have concluded that the desert grasslands of the Southwest have been invaded by woody species as a direct or indirect result of overgrazing (e.g., Smith, 1899; Bray, 1901; Clements, 1934; Allred, 1949; Gardner, 1951; Parker and Martin, 1952; Glendening and Paulsen, 1955). In almost solitary opposition, Malin (1953) attempts to show from historical records that woody species, particularly mesquite (Prosopis spp.), have not extended their area in historic times, although he concedes that some mesquite stands have become denser.

Parker and Martin (1952), in discussing the invasion of southern

Arizona rangelands by mesquite, point out a number of causes for the advance of these woody plants: reduction in grass cover from overgrazing and drought[1], cessation of range fires, and dissemination and planting of seed by livestock and wild animals. They state that species of mesquite dominate the vegetation on more than 70 million acres in the Southwest and estimate conservatively that at least half this vast area has been occupied during the past 100 years. These authors and Glendening and Paulsen (1955) show that, although grasses tend to suppress young mesquite plants, once the shrubs get established they continue to increase in number and crown spread while cover of grass declines. Except with half shrubs like *Aplopappus tenuisectus* (Humphrey, 1937; Canfield, 1948; Brown, 1950), it appears that mere cessation of grazing and increase of grasses will not reverse the trend from dominance by woody vegetation. Haskell (1945) found little change, even in *A. tenuisectus,* however, after 18 years of conservative grazing near Oracle, Arizona.

Glendening (1952) shows that four species of cactus have increased on the Santa Rita Experimental Range in southern Arizona, regardless of grazing treatment. He suggests that the increase of mesquite has had a tendency to dry the soil of a former grassland site and, as reflected by the invasion of true desert species, to transform it essentially into a desert site.

Cactus, mainly Opuntia spp., may become an important part of Plains vegetation, not only in desert grassland but in mixed-grass and true prairie, particularly during periods of drought (Weaver and Albertson, 1940, 1944). Although increase in cactus is sometimes attributed directly to overgrazing, on the western Plains Turner and Costello (1942) could detect neither differences in trend over five- and six-year periods between two areas of grazed and protected range, nor in abundance of cactus between 13 areas that had been protected from grazing for ten to 40 years and comparable range subject to heavy use. This may not have been an adequate test; as noted above, the increase of herbaceous vegetation following cessation of grazing does not necessarily cause a decrease of established woody plants.

[1] The basis for assigning this role to drought is obscure. That disturbance of the grass cover should favor woody invaders is understandable, but that thinning of the grass cover by drought should favor the establishment of a shrub like mesquite seems doubtful. It is possible, of course, that drought might encourage the spread of some woody plants with exclusively superficial root systems, like the cacti, and not others like mesquite and juniper.

In Kansas Cook (1942) concluded that three insects, most important of which was a moth, *Melitara dentata,* keep *Opuntia humifusa* in check during years of moderate or abundant rainfall, but that the decline of the moth during drought enables the cactus to increase and take advantage of bare areas created by the death of herbaceous vegetation. Cook observed that cactus in areas having a dense herbaceous growth tended to be much more heavily infested by moth larvae than cactus in overgrazed areas lacking such herbaceous growth. Holscher (1944), observing *O. polyacantha* in eastern Montana following the drought of the thirties, reached a similar conclusion.

Miller (1921) noted the aggressive invasion of grassy openings by juniper in northern Arizona; and from growth rings he showed that the invasion began shortly before 1900. Leopold (1924) also described the aggressive spread of juniper and other woody plants in Arizona, and correlated this spread with cessation of range fires, overgrazing and accelerated erosion since settlement. Thinning of the grass cover and exposure of bare soil by overgrazing is believed by Parker (1945) to be the principal cause for the spread of juniper. This conclusion is corroborated by an observation in Texas of 2.3 times as many "cedar trees" per acre on range in fair condition as on range across the fence in good condition (Mann and Hayes, 1948).

The spread of juniper in Texas is attributed by Wolff (1948) to thinning of the grass cover by overgrazing and dissemination of the seeds through birds, jackrabbits, cottontails, foxes, coyotes and other wild animals. In Arizona Miller (1921) attributed the dissemination of juniper seed to sheep, but in Texas Wolff did not find much evidence to indicate that domestic livestock were a material factor in dissemination.

The aggressive spread of woody plants brings up the highly controversial question of the importance of fire in maintaining grassland, particularly desert grassland. The question, put another way, is whether a particular grassland is truly climax or whether it is subclimax to woodland or forest. It must be recognized that two effects of overgrazing, which are almost inextricably associated, are involved in the invasion of woody plants. One is a reduction in fuel, the other a reduction in competing ability of the herbaceous vegetation. Thus it is quite possible that, lacking an independent evaluation of the reduction in vigor and of the opening of stand of the herbaceous plants, the influence of fire has been overrated, at least for some species. Fire is effective in reducing some woody species, but not others, particularly sprouting forms. Reynolds and Bohning (1956) obtained a much greater fire kill of *Aplopappus tenuisectus* and various cacti than of mesquite. Glendening and Paulsen (1955) were able to kill an appreciable proportion of only the smallest mesquite plants with fire. Evidence that plant competition is more important than fire is provided by Rummell's (1951) observation of aggressive ponderosa pine reproduction in an overgrazed park in eastern Washington as compared with very little in a comparable park in virgin condition. Neither area had been completely burned over for at least 125 years.

It seems quite possible that the invasion of grassland by trees in the broad, irregular transition from forest to prairie in the Middle West, which has aroused the curiosity of many ecologists (e.g., Cowles, 1928), may have been caused by a factor seldom suggested—overgrazing of the settlers' livestock.

The death of woody plants in grassland during drought is doubtless valid evidence that they are invaders because of some abnormal disturbance such as overgrazing. Death of oaks has been noted particularly, e.g., at the prairie edge in Illinois during the 1913-1914 drought (Transeau, 1935), at the western edge of the Western Cross Timbers in Texas during the great drought of the 1930's (Dyksterhuis, 1948), and in the Edwards Plateau region of Texas during the 1949-1954 drought (Young, 1956). This last account is of interest here because of the observation (although without comparative data) that death of woody plants was more pronounced on lightly grazed ranges having vigorous herbaceous cover than on heavily grazed ranges where the herbaceous cover was depleted. The observation is also made that, in addition to several species of oak, Ashe juniper was hard hit by drought, but not mesquite or pricklypear.

Although death from drought may be valid evidence of abnormal invasion, survival is not necessarily evidence that a woody species belongs in the grassland in which it occurs. It appears that some deep-rooted woody species, such as mesquite, once they have become well established, are in the grassland to stay. It would appear that the failure of a woody plant in herbaceous vegetation occurs normally in the seedling stage. Thus, although its dying is evidence that it is an invader, its survival, after a woody species has become established, is not necessarily evidence that it is part of the natural vegetation.

SOUTHERN DESERT SHRUB

In a southern desert shrub type near Tucson, Blydenstein *et al.* (1957) noted considerably greater frequency of occurrence of grasses and such palatable shrubs as *Krameria grayi* after 50 years of protection than under grazing. At the same time there was appreciably less of the unpalatable *Franseria deltoidea.* These facts suggest that the "occasional light use" this range receives has had an appreciably detrimental effect.

PACIFIC PRAIRIE

Burcham (1957) has combined a historical and ecological approach to describe trends that have taken place on California rangelands. The original Central Valley prairie in California was dominated by bunchgrasses, mainly species of Stipa, and contained numerous species of annual and perennial forbs. The north coastal prairie, a more mesophytic, discontinuous grassland on ridges and dry exposures, was also made up of perennial bunchgrasses and forbs. The basic reason for the wholesale replacement of the native species by a vegetation dominated by Mediterranean annuals was abusively heavy grazing which reached its peak in the beginning of a period of severe drought that culminated about 1863.

Burcham gives evidence to show that there have been four stages in a historical succession in which progressively less palatable annuals have replaced more palatable species. These stages the author relates to contemporary stages of a descending scale of plant succession on California rangelands under different intensities of use. The first stage, characterized by *Avena fatua, A. barbata* and *Brassica nigra,* was most prominent between 1845 and 1855. The second stage, characterized by *Erodium cicutarium, Hordeum leporinum, Gastridium ventricosum* and native annuals like *Festuca megalura,* was dominant from about 1855 to 1870. The third stage, in which introduced species of Hordeum, *Bromus rubens, Aira caryophyllea* and a number of forbs were dominant, began to be conspicuous between 1870 and 1880 and is widespread today. The fourth stage, now evident in some areas, is characterized by such undesirable species as *Elymus caput-medusae, Aegilops triuncialis, Brachypodium distachyon, Cynosurus echinatus* and Hypochaeris spp. In short, from the time the original vegetation was destroyed by overgrazing 100 years ago, the successional sequence has been one of continuing depletion, of replacement of less desirable forage species by invading species even less desirable.

This is a black picture of plant succession under grazing, but Burcham does suggest constructive possibilities under management. He gives an example of how a range in San Diego County was greatly improved by rotational grazing. The plan was to handicap certain early-maturing undesirable annuals by heavy grazing in early spring when herbage production was not yet well advanced. These include annual species of Festuca and Hordeum, together with *Bromus rigidus, B. rubens, Gastridium* and *Aira.* Such heavy grazing inhibits seed production by these plants but does not greatly handicap seed production by somewhat later-maturing, more desirable plants, including *Bromus mollis* and species of Avena, Lolium, Erodium, Medicago, Trifolium and certain native and introduced perennial grasses. These species, which develop during the period of most rapid growth, are not grazed so heavily, since the number of stock that grazes heavily in early spring is not sufficient to utilize the greater volume of forage that develops later. Finally, because of the depletion of soil moisture by the desirable species, certain later-maturing undesirable plants, including *Elymus caput-medusae* and species of Aegilops, Cynosurus, Madia and Hemizonia, are handicapped.

This last point is hard to understand because elsewhere the author points out that "frequently late rains provided moisture for additional growth of perennials after grazing ended in May". If this late-spring moisture helps the perennial grasses, why doesn't it also help the low-value weeds of early summer, midsummer, or later? Two things are lacking in the evidence presented as to the causes of the trend observed, an exact quantitative comparison and an evaluation of other factors, such as precipitation, that might have influenced it.

Sampson *et al.* (1951) and Sampson (1952), following an earlier study (Sampson, 1919), present successional scales for California foothill annual and mountain perennial ranges. These are correlated, at least by implication, with parallel stages of soil development, but no observational evidence for these parallel successions is given.

Under total protection of a highly productive annual range in the woodland type of the foothills of California there was a complete reversal of plant composition in two years, from a 98-percent cover of forbs to a 96-percent cover of grasses (Talbot *et al.,* 1939; Talbot and Biswell, 1942). Erodium spp. dropped from over 80 percent to three percent of the cover under complete protection, to 14 percent where cattle were excluded but not rodents, and only to 50 percent on range grazed both by livestock and rodents. Under total protection *Bromus rigidus* became dominant in the fourth and fifth years, but this undesirable species made up less than one percent of the cover at all times where either rodents, or livestock and rodents, were present. From such studies Bentley and Talbot (1951) came to the conclusion that the most desirable composition of this annual vegetation is maintained by some grazing. If the range is grazed lightly or not at all, there is a tendency for tall annual grasses to increase and shade out Erodium, Trifolium and other valuable, low-growing plants.

PALOUSE GRASSLAND

This very complex association extends from northern Utah and southern Idaho through eastern Oregon and Washington, and 250 miles into the southern interior of British Columbia. It has been divided into a relatively moist Festuca zone and a drier Agropyron zone (Weaver, 1917; Daubenmire, 1942, 1952). On dry sites and toward the southern end of its area this association merges imperceptibly into the sagebrush association of the northern desert shrub formation (Shantz, 1925). As a result of livestock overgrazing, the herbaceous components of the sagebrush association have diminished and the proportion of sagebrush has increased (Blaisdell, 1953), and sagebrush has tended to invade the drier parts of the Palouse grassland. (Stoddart, 1941).

Tisdale's (1947) analysis of changes due to overgrazing in the grasslands of southern British Columbia is probably the most comprehensive treatment available. The effect of overgrazing in the moister zone has been to reduce *Agropyron spicatum* and *Festuca scabrella* and to encourage the increase or invasion of *Stipa columbiana, Poa secunda, Bromus tectorum* and the vegetatively spreading species, *Poa pratensis, Achillea lanulosa* and *Antennaria parvifolia* in what Tisdale calls the Stipa-Poa and the Poa-Bromus associes. Farther south in eastern Washington *Festuca scabrella* drops out of the climax and *F. idahoensis* becomes codominant with Agropyron. Forbs form a greater proportion of the climax cover, and scattered, dwarfed, shrubs (Prunus, Rosa, Symphoricarpos) become somewhat more conspicuous (Daubenmire, 1952).

In the drier (Tisdale's Agropyron-Poa) zone the dominant species are *Agropyron spicatum* and *Poa secunda.* Two communities that have developed as a result of overgrazing are the Stipa-Agropyron-Poa and the Bromus-Poa-Stipa associes, the latter representing the more severe depletion. Tisdale notes that, if light grazing is practised in the Bromus associes, the perennial grasses increase and Bromus declines. This has been observed widely elsewhere in the Intermountain region (Pickford, 1942). Vegetation in this zone as far south as northern Utah and as far east as south-central Montana appears to react similarly to grazing pressure and fire—toward dominance of *Artemisia tridentata* and *Bromus tectorum* (Stoddart, 1941; Humphrey and Lister, 1941; Young, 1943; Humphrey, 1945a, 1945b; Wright and Wright, 1948).

Daubenmire (1940) concluded that the "biotic climax" under sheep grazing in southeastern Washington was not a stand dominated by *B. tectorum* but one dominated by *Poa secunda* and small annual forbs. Since the response of the vegetation was different than that of similar vegetation elsewhere in the Intermountain West, Daubenmire suggested that environmental conditions in southeastern Washington might be somehow atypical. It seems more reasonable to suggest that his example of a "biotic climax" is range that is more intensively and severely grazed than usual, for Piemeisel (1945) has shown in southern Idaho that annual forbs can be maintained, and *B. tectorum* kept from achieving dominance, by such recurrent disturbance as the close grazing of jackrabbits.

In the same general area in which Daubenmire worked, Young (1943) indicates that both on the moist Festuca type and the dry Agropyron type these grasses give way under grazing pressure (whether cattle or sheep is not specified) to species of such forbs as Lupinus, Potentilla, Lomatium, Astragalus and Achillea, the shrub *Chrysothamnus nauseosus,* and the grasses *Bromus tectorum* and *Poa secunda.* Bromus may comprise as much as 90 percent of the vegetation.

It is an interesting fact that *B. tectorum* was not mentioned by Weaver (1917) who studied the Palouse grassland from 1912 to 1914. It is given conspicuous recognition by all the later authors that have been cited. This aggressive Mediterranean annual, evidently aided by livestock grazing and probably imported repeatedly from the sagebrush association where it had become a dominant, made itself at home in the Palouse grassland within 25 years.

NORTHERN DESERT SHRUB

SAGEBRUSH ASSOCIATION

The extent and character of the sagebrush association in pristine condition will probably never be known accurately. The association covered much of the plains and foothills of the Intermountain West. It occupied the area that was most heavily grazed by domestic livestock soonest after settlement, and much of it has since come under cultivation. Probably it was for the most part an open stand of shrubs, with a highly diversified understory of perennial grasses and forbs (Blaisdell, 1953). As a result of disturbance, mostly by overgrazing, it appears that sagebrush has extended into other types where its existence is marginal. This is suggested by an example of change in north-central Wyoming in which sagebrush was strongly reduced as grasses increased after only eight years of moderate grazing and deferment during the grazing season (Cooper, 1953). Another example is derived from the death of sagebrush in association with grass in southeastern Montana, because of drought and grasshoppers, in contrast to its survival on overgrazed range (Allred, 1941). Still another example to similar effect is Tisdale's (1947) observation in the Tranquille Range of British Columbia, that *Chrysothamnus nauseosus* decreased markedly, and *Artemisia tridentata* somewhat less markedly, during four years of reduced grazing with a concomitant increase in grasses.

It is going too far, however, in this reviewer's opinion, to consider this association to be properly grassland, and the presence of sagebrush throughout essentially its entire area to be a result of man's disturbance, as Clements and Clements (1941) do.

In eastern Idaho it has been shown that spring grazing by sheep depletes the herbaceous components of the sagebrush association and increases the sagebrush (*A. tripartita*); but that heavy fall grazing by sheep, after the herbaceous species have dried, favors them rather than the sagebrush (Craddock and Forsling, 1938; Mueggler, 1950). Mueggler's data suggest that under fall sheep grazing *A. tripartita* formed about the same proportion of the vegetation in 1949 as in 1924, but the presence of many dead *A. tripartita* plants in the fall-grazed area indicates that the sagebrush has in fact declined. It would appear that a comparison of proportions based upon cover in 1924 and upon weight in 1949 obscures this essential change. This inference is supported by the fact that, at the end of six years of reversed treatments, there has been a perceptible reversal in effect, which indicates that the *A. tripartita* and other shrubs are indeed reduced, and the more palatable herbaceous components of the vegetation increased, by fall grazing (Jack E. Schmautz, personal communication). This is one of the few instances known to the reviewer where grazing pressure can be applied under range conditions to achieve improvement of the forage. It appears that fairly heavy late fall grazing, with light grazing in spring under a rotational system, will favor and maintain the herbaceous vegetation and hold the shrubs in check.

The fact that under heavy grazing most palatable grasses and forbs are reduced and sagebrush increases has been recorded by many authors (Pickford, 1932; Cottam and Stewart, 1940; Shantz and Piemeisel, 1940; Tisdale, 1947; Bleak, 1948). Where they occur in proximity to the sagebrush association, juniper and pinyon may invade areas with deep soil occupied by sagebrush or herbaceous vegetation (Cottam and Stewart, 1940; Woodbury, 1947), just as they invade desert grassland. The reason is evidently heavy grazing's weakening the herbaceous vegetation and reducing the supply of fuel. In general, heavy grazing by sheep in the sagebrush association reduces forbs, such as Lupinus, Balsamorhiza and Penstemon, more completely than the perennial grasses, whereas heavy grazing by cattle has the reverse effect.

Ecological effects of overgrazing in the sagebrush-grass type are complicated by the effects of fire and cultivation. *A. tridentata* is very sensitive to fire, and fire can be utilized to reduce it and make herbaceous forage more readily available (Blaisdell, 1953). However, fire has many undesirable effects, one of which, coupled with overgrazing, is to encourage the spread and dominance of cheatgrass, *Bromus tectorum* (Hull and Pechanec, 1947; Robertson and Kennedy, 1954). On sagebrush-cheatgrass range there appears to be a continual tug of war: sagebrush persistently reinvades, but recurrent fires maintain dominance of the annuals.

The relations between annual species induced as a result of cultivation, fire and overgrazing have been carefully studied over many years and analyzed by Piemeisel (1938, 1945, 1951). Piemeisel's studies show that any extreme disturbance that results in denudation of the perennial plant cover is followed by a regular sequence of annual plant communities: two years of dominance by *Salsola kali* followed by two years of dominance by annual mustards (Descurainia, Sisymbrium), and from the fifth year onward dominance by *Bromus tectorum.* This time scale of annual succession, which is very little affected by fluctuations in weather, depends upon freedom from disturbance. The sequence can be interrupted and held back by such disturbances as excessive livestock grazing or feeding of jackrabbits. Over a longer period, and depending upon the availability of seed of sagebrush and perennial grasses, Bromus is eventually replaced by these.

SHADSCALE ASSOCIATION

This association includes a variety of desert communities dominated by widely spaced low shrubs. The principal genera are Atriplex, Artemisia, Eurotia, Chrysothamnus, Grayia, Kochia and Sarcobatus. Grasses are sparsely dispersed—Oryzopsis, Hilaria, Sitanion, Stipa, Bouteloua—and perennial forbs are not numerous, the most common, perhaps, being species of Sphaeralcea. Annual forbs and grasses may be conspicuous in especially wet growing seasons. *Salsola kali* has recently become widespread as a consequence of depletion of plant cover (Stewart, *et al.* 1940). Shantz and Piemeisel (1940) observed that by 1915 Salsola was still restricted to parts of Escalante Valley, Utah, and noted that in 1912 Kearney *et al.* (1914) had not recorded this species at all in Tooele Valley. Still more recently, spread of the poisonous *Halogeton glomeratus,* an annual similar to Salsola, has received considerable notoriety. *Bromus tectorum* may be locally dominant where grazing has reduced or eliminated the desert shrubs.

The shadscale association is used primarily for winter range, particularly by sheep. Because of soil salinity and low precipitation, areas dominated by this vegetation are not widely used for crop agriculture. This is in contrast to the area of the sagebrush association which, because of generally fertile soils and greater precipitation, is the most important area of cultivated land in the Intermountain region.

Stewart *et al.* (1940) surveyed two desert valleys in western Utah, one of which had been much more severely grazed over a longer period than the other. They compared numbers of living and dead plants by types and age-class distributions, and came to the conclusions that heavy grazing was destroying *Oryzopsis hymenoides* and *Grayia spinosa,* and had greatly reduced the quantity of *Eurotia lanata* and *Artemisia nova.* As Shantz and Piemeisel (1940) had observed in 1915, they concluded that *Chrysothamnus stenophyllus* was replacing, and Salsola had replaced, more valuable species over extensive areas.

Protection or moderate grazing over a period of years has confirmed and extended these earlier observations (Hutchings and Stewart, 1953) by establishing trends in which the palatable species have increased while less palatable ones have declined. Such changes have taken place under managed grazing, even though the herbage of a palatable species like *Artemisia nova* is utilized 65 percent, while that of *Chrysothamnus stenophyllus* is utilized only ten percent. Differences in trends are of course most marked in contrasts between severe grazing and moderate grazing or protection. On experimental pastures where differences in utilization were not great, only trends of production of Eurotia showed marked differences in response to use-intensity. Over a 13-year period the increase of Eurotia under moderate grazing was faster than under either light or heavy grazing. Possibly the increase was faster under moderate than under light grazing because there was markedly less Eurotia in the lightly grazed pastures to begin with and therefore not much difference in utilization intensity.

MOUNTAIN RANGELANDS

MOUNTAIN BRUSH AND CHAPARRAL ZONE

The effect of intensive livestock grazing on the lower mountain slopes, dominated in Utah by *Quercus gambelii* and other tall shrubs, has been to reduce the proportion of herbaceous vegetation and the more palatable shrubs and to increase the proportion of less palatable species (Forsling and Storm, 1929; Cottam and Evans, 1945). The abundance of grass on scrub-oak range used in common by deer and cattle is inversely correlated with intensity of cattle utilization (Julander and Robinette, 1950), so that scarcity of *Agropyron spicatum* may be used as an indicator of the degree of cattle use. In the *Cercocarpus ledifolius* type in Utah, heavy grazing in spring and fall by either sheep or cattle reduces the production of perennial forbs and grasses (and because of increased bare ground, increases the annuals), and increases the volume of the relatively unpalatable *Artemisia tridentata.* On the other hand, heavy winter grazing by deer in the same type reduces the productivity of *C. ledifolius,* a favored deer forage, but does not alter the productivity of perennial forbs and grasses materially, and, as a result, does not increase the proportion of annuals (Julander, 1955).

In the pinyon-juniper woodland of northern Arizona, excessive browsing by deer has reduced shrubby vegetation and favored the growth of herbaceous species less readily eaten by deer. In places most of the plants of *Cowania stansburiana* had been killed during the Kaibab irruption. At higher elevations, in the ponderosa pine and spruce-fir zones, much of the *Ceanothus fendleri,* Symphoricarpos, Rubus and Salix had been killed, and all recent aspen sprouts (*Populus tremuloides*) were grazed back closely (Rasmussen, 1941).

MONTANE FOREST ZONE

On heavily grazed ponderosa pine range in northwestern New Mexico, Gardner and Hubbell (1943) noted that the invading rubberweed, *Actinea richardsoni,* had declined after eight years of protection, while certain other species had increased. Perhaps because of the insensitivity of frequency data as a measure of change, no difference could be detected between trends on completely protected and lightly grazed range.

In northern Arizona the invasion of heavily grazed grassy openings by pine has been conspicuous (Leopold, 1924; Pearson, 1936). Pearson (1923) noted that seedlings of *Pinus ponderosa* were more likely to grow vigorously where herbaceous vegetation was grazed than where the grass was thick. On the basis of these observations and studies in which competing grasses were variously reduced, he concluded that very heavy grazing when a good cone crop was in evidence and during the following year of seedling establishment should be an effective silvicultural tool (Pearson, 1934, 1942, 1950). Most emphasis in early studies by foresters was on the damage done by grazing, especially sheep grazing, to pine reproduction (Hill, 1917; Sparhawk, 1918; Jardine, 1920; Pearson, 1923; Loveridge, 1924). That such damage to pine reproduction was so serious is probably an accurate reflection (by present-day standards) of the customary severity of grazing practiced when the West was young.

In central Washington a positive relation between reproduction of *P. ponderosa* and heavy grazing has also been reported by Rummell (1951) who compared an area that had never been grazed by domestic livestock with one that had been heavily grazed for 40 years. Rummell concluded that livestock overgrazing is more important in fostering the successful establishment of young trees than freedom from fire. The most striking effect of heavy grazing, in addition to encouraging pines in grassy openings, was the reduction of grasses, principally *Calamagrostis rubescens*, to half or less of the cover they formed on the virgin range.

Johnson (1956) compared the effects of four degrees of forage utilization by cattle on vegetation in ponderosa pine parkland in central Colorado. As such comparisons usually show, heavy grazing (utilization of 50 percent or more of palatable grass and sedge herbage) damaged the more palatable species and tended to encourage the unpalatable ones. Fortunately for our purpose, the study includes comparisons of production of vegetation under protection for ten years as well as under light (10 to 20 percent) and moderate (30 to 40 percent) utilization of palatable grasses and sedges. The most abundant palatable grasses were *Muhlenbergia montana* and *Festuca arizonica.* Other palatable species that were markedly less abundant were Carex spp., *Andropogon scoparius* and *Astragalus goniatus.* Species of comparatively low palatability were *Bouteloua gracilis, Antennaria rosea, Artemisia frigida* and *Erigeron flagellaris.*

In general, the production of palatable species tended to be higher under protection than under light or moderate use, and with one notable exception the production of unpalatable species tended to be lower. This exception was *Artemisia frigida* which was more productive on protected areas than on any of the grazed range and in greater number than on either the moderately or lightly grazed range. No explanation is offered for this anomaly. In short, although the differences between no grazing and light or moderate grazing are by no means clear-cut, many of them seem sufficiently marked to be real. They give no suggestion that light or moderate grazing has a positive effect in furthering succession toward the climax, as opposed to no grazing at all, but instead, a retarding effect.

Pickford and Reid (1948) distinguished two levels of range condition in ponderosa pine openings in eastern Oregon, pointing out that these openings are more heavily grazed than areas overshadowed by timber and therefore are likely to be rapidly depleted. In bunchgrass openings in good condition more than 50 percent of the ground is covered by vegetation. The dominant species are *Agropyron spicatum, Festuca idahoensis* and *Koeleria cristata.* In good-condition, dry-meadow openings the cover is almost complete and consists mostly of *Agrostis diegoensis, Poa pratensis* and *Festuca rubra.*

Using range-survey techniques, mountain meadows in eastern Oregon and Washington are arranged by the same authors (Reid and Pickford, 1946) into four condition classes relating to depletion from overgrazing. Good- or excellent-condition meadows have a two-thirds cover, mostly of perennial grasses and sedges, with *Deschampsia caespitosa* overwhelmingly dominant. On very-poor-condition meadows vegetation covers only about one-tenth of the ground surface, and nearly two-thirds of it is made up of annual grasses and forbs. Similar classifications have been made for Sierra Nevada wet meadows (Crane, 1950) and for mountain grasslands in southwestern Alberta (Hanson, 1951).

SUBALPINE ZONE

The subalpine zone of the Wasatch Plateau in central Utah was the site of an early successional study by Sampson (1919). This high-elevation herbland had been virtually denuded by uncontrolled and exploitative overgrazing from about 1870 to 1905, and attention was directed to the devastated condition of the range by mud-rock floods that damaged settlements at the canyon mouths. A. W. Sampson, who laid out the pioneer study that has demonstrated the important influence of herbaceous vegetation in controlling erosion and floods (Sampson and Weyl, 1918; Forsling, 1931), devised a successional scheme in four stages and inserted these between an assumed forest climax at the top and early stages of soil formation from parent rock at the bottom. Since several successional studies in relation to grazing have been patterned on this model, it will be examined in some detail here.

The lowest stage treated by Sampson (1919) in any detail was the first-weed stage or "ruderal-early-weed consociation" in which the dominants were annual weeds of such genera as Chenopodium, Collomia, Madia, Orthocarpus and Descurainia. The next higher (second weed) stage was the "foxglove-sweetsage-yarrow consociation" in which the chief dominants were *Penstemon rydbergii, Artemisia discolor* and *Achillea lanulosa.* The third, the mixed-grass-and-weed stage, referred to as the "porcupinegrass-yellowbrush consociation", contained many species but had *Stipa lettermani* and *Chrysothamnus viscidiflorus* as principal dominants. The fourth stage was the herbaceous climax, the "wheatgrass consociation", dominated by either bunch wheatgrass (*Agropyron trachycaulum*) or turf wheatgrass (*A. dasysta-*

chyum). In this sequence, and in its relations to successional stages above and below it, Sampson made no distinction between primary and secondary succession and emphasized the reversibility of the process—i.e., that "retrogressive" succession proceeds through the same stages as "progressive" succession but in reverse order.

Ellison's (1954) treatment of succession in the same area differs sharply from Sampson's in most respects. It agrees in the essential characteristics of the first-weed stage on denuded soil surfaces, which Ellison refers to as "communities of ephemerals". He considers the communities of perennial species, which were arranged by Sampson into three successive stages, as essentially equivalent, determined primarily by grazing pressure—those dominated by grasses reflecting overgrazing by sheep, and those dominated by forbs reflecting overgrazing by cattle. He shows that the ranges of many of the species dominant in these grazing-induced communities have increased in the subalpine zone, and that some of these species have evidently been introduced from elsewhere. Not all the invading species are unpalatable. *Taraxacum officinale,* for example, is relished by sheep, but because of its rosette habit and precocity in flowering and fruiting, together with the suppression of taller vegetation by severe grazing, Taraxacum flourishes on heavily grazed sheep range.

The original herbland, instead of being dominated by wheatgrasses, Ellison considers to have been a rich mixture of tall, rather succulent forbs, grasses and sedges, making nearly a complete cover of vegetation and litter, and with the following species dominant: *Mertensia leonardi, Agropyron trachycaulum, Valeriana occidentalis, Osmorhiza occidentalis, Heracleum lanatum, Angelica pinnata, Polemonium foliosissimum, Erigeron speciosus, Bromus carinatus, B. anomalus, Carex festivella, C. hoodii, C. raynoldsii, Aquilegia coerulea, Castelleja sulphurea, C. leonardi.*

Ellison distinguishes between primary succession, in which soil formation is involved, and the much more rapid changes that take place upon a developed soil in the course of secondary successions. He shows that the sequence of events in primary succession and soil development in the subalpine zone of the Wasatch Plateau are very different, indeed, from the changes brought about by overgrazing. On the basis of comparative soil development, he shows that on warm, dry exposures the herbaceous vegetation could not be subclimax to spruce-fir forest, but that, if the communities were sequentially related at all, the tree-dominated community must be the more primitive. Finally he distinguishes changes involving accelerated soil erosion as "destructive change" in contrast to ordinary succession, pointing out that "It is ruinous for the range manager to be guided by the belief that vegetal changes associated with accelerated erosion are the counterpart of normal, primary succession, and that accelerated erosion is merely the counterpart of normal soil development".

On the basis of range-survey data, Pickford and Reid (1942) present a successional sequence much like Sampson's for the subalpine herblands of the Wallowa and Blue Mountains of eastern Oregon. The climax grassland is considered to have been dominated by one species, *Festuca viridula,* in virtually a pure stand and forming a nearly complete cover. Below this is a transition stage, a mixed-grass-and-weed type in which cover is only 20 to 40 percent of that in the *F. viridula* type, and in which the following species are most abundant: *F. viridula, Stipa columbiana,* Carex spp., *Lupinus leucophyllus, Gilia nuttallii,* Eriogonum spp., and *Artemisia tridentata.*

Next lower on the successional scale is the second-weed stage, the weed-needlegrass type, which seems very little different from the transition stage, having a somewhat lesser cover and smaller proportions of the same species. *Agastache urticifolia* was important in this stage in the Wallowa Mountains, and *Polygonum phytolaccaefolium* in the Blue Mountains.

In this successional scheme accelerated soil erosion and stage of succession are considered to be correlated. Soil losses in the *F. viridula* type are estimated to have been about two tons per acre during the lives of existing *F. viridula* plants, a rate considered by the authors to approximate the geologic normal. This is in marked contrast to the reviewer's conception of normal erosion in the subalpine zone in central Utah as being, except for land slips, essentially imperceptible. Losses in the mixed grass and weed stage are estimated to have been between 212 and 606 tons per acre, and in the second weed stage 927 tons per acre. Although the destructive nature of accelerated soil erosion is recognized, its incongruity as part of a successional scale is not.

EFFECTS OF HERBAGE REMOVAL FROM INDIVIDUAL PLANTS

Although the influence of grazing may be exerted in many ways—trampling, fertilizing the soil, introducing plants from some other area through dissemination of seed—the most obvious influence is that of reducing the volume of herbage and the area of photosynthetic surface. Many studies have sought to evaluate the influence of grazing by clipping herbage artificially to various degrees and at various times during the plant's growth cycle. The advantages and disadvantages of clipping studies have been discussed by Culley *et al.* (1933) who conclude that, although clipping does not simulate grazing precisely, it can be a useful tool when applied with judgment in connection with studies of actual grazing.

In this section we shall consider the effects of clipping on the individual plant—first in the greenhouse, then in the field. Most of the clipping studies in which an interaction of different species is involved have been considered under the effects of grazing in the major range types. For the most part, we shall not concern ourselves with clipping studies of humid pastures. These have been reviewed recently by Wagner (1952).

GREENHOUSE STUDIES

Conditions for plant growth in the greenhouse are presumably optimum, particularly because moisture stress can be minimized. Nevertheless, greenhouse studies show that reduction of photosynthetic surface by clipping reduces production of both herbage and roots as compared with those of unclipped controls (Robertson, 1933; Carter and Law, 1948; Branson, 1956). The more frequent or more severe the defoliation, the more markedly production is depressed. Biswell and Weaver (1933) concluded that frequent clipping not only reduced the production of prairie species but lowered their resistance to freezing because clipped sods that had been frozen and planted recovered much more slowly than control sods.

Among many investigators to demonstrate lowered production following clipping were Parker and Sampson (1931) who used *Stipa pulchra* and *Bromus hordeaceus* plants in nutrient solution. They observed that regeneration of tops was immediate after harvesting with a sharp acceleration in growth of leaf blades for about 24 hours, and that then the rate of elongation declined, as compared with the rate on unharvested plants. They also noted that root growth of Stipa ceased for nearly 15 days, and of Bromus for eight days after harvesting.

Root mortality of plants that are severely clipped may be high. This was demonstrated by Weaver and Zink (1946) and Weaver and

Darland (1947) who marked numerous roots with metal bands, imposed clipping treatments in the greenhouse for part of a growing season, and then appraised the mortality of roots of clipped and unclipped plants.

In Parker and Sampson's study, single harvestings did not appear to reduce root yields more than top yields. In close and repeated harvestings, however, root production is the more markedly reduced. A thorough review of the effects of herbage removal on roots is given by Troughton (1957). In practically every study, the effect of herbage removal has been reflected in reduced root production.

Elongation of tops is often stimulated by clipping (Parker and Sampson, 1931; Robertson, 1933; Branson, 1956) so that cumulative height growth of plants frequently clipped tends to be greater than that of unclipped plants. Inasmuch as root production is the more markedly reduced by clipping, it would appear that the stimulated regrowth of foliage is made at the expense of root growth. Thus the roots of a grazed plant are probably handicapped, as compared with those of an ungrazed plant, in competing for soil moisture.

Most studies have shown that clipping tends to reduce or retard tillering in grasses (Finnell, 1929; McCarty, 1932; Robertson, 1933; Hubbard and Harper, 1949; Cook and Stoddart, 1953; Sprague, 1954; Branson, 1956). Leopold (1949), however, demonstrated in one experiment that removing the shoot apices stimulated tillering in teosinte and barley, and concluded that auxin produced at the shoot apex inhibits tillering. These apparently contradictory results may be reconciled if it is assumed that little tissue was destroyed in Leopold's experiment and that in the other experiments the influence of auxin was overshadowed by the damage done in clipping.

In most experiments the clipping treatments are severe. Usually the plants are harvested completely or clipped to a height of about an inch. Crider's (1955) studies on root growth in response to clipping are particularly interesting because they include some light treatments. *Chloris gayana* plants 64 days after seeding were clipped once to remove 10, 20, 30, 40, 50, 60, 70, 80 and 90 percent of their tops by volume. As compared with growth of roots of the control plants 33 days later, growth of roots of all clipped plants was checked—least by the 10 percent and most by the 90 percent clipping. That total root production under 10 and 20 percent clipping was significantly less than that of the unclipped controls may be questioned, but the consistency of the decline with degree of clipping suggests that the effect is a real one. The study indicates that no level of harvesting, not even the lightest, encourages root production in Chloris, even though there is a suggestion of some stimulation within a week after clipping at the lightest intensities.

The retardation of production of main roots was not directly proportional to degree of defoliation but became intensified as defoliation increased. The depression of root production from zero to 20 percent defoliation, for example, was not so marked as the depression of root production between 60 and 80 percent.

Like Parker and Sampson (1931), Crider showed that severe defoliation resulted in complete stoppage of root growth. Unfortunately for our purpose, Crider did not include an appraisal of clipping intensity on production of herbage.

FIELD CLIPPING OF HERBS

In three prairie and four pasture types near Lincoln, Nebraska, Weaver and Hougen (1939) demonstrated the harmful effect of frequent clipping on *Andropogon scoparius* and *A. gerardi* in terms of production the year following treatment. During the first year of treatment, production of the two Andropogons was as great on the clipped quadrats as on controls clipped at the end of the season. The yields of underground parts were smaller for plants that had been closely and repeatedly clipped than for unclipped plants. Bukey and Weaver (1939) showed that severe clipping decreased the percentage of certain carbohydrates in these roots.

It may be wondered why clipping carried out in the field, particularly during the drought year 1934, should not show more marked depressions of yields than the greenhouse study by Biswell and Weaver (1933). The reasons are probably that the intervals between clippings in the greenhouse study were shorter, and that growth was 10 to 30 times as fast in the greenhouse as in the open, doubtless exhausting root reserves more completely than slower growth in the field.

From observation of prairie species, Branson (1953) suggests that a high growing point and a large proportion of reproductive to vegetative shoots make a species susceptible to damage from grazing—two qualities that the same species may not possess. Thus the growing points of the *Panicum virgatum* and *Agropyron smithii* studied reached a height of 20 inches by the end of summer, whereas those of *Andro-*

pogon scoparius were only an inch above the ground; while, on the other hand, Panicum and Andropogon had two or three flowering stems to every vegetative stem, whereas Agropyron had only one reproductive stem in 17. In this comparison, Panicum, having two counts against it, should be the most susceptible to grazing damage. The resistant short grasses and *Poa pratensis* have small proportions of flowering stems as well as low growing points.

Newell and Keim (1947) compared the effects of mowing at monthly intervals with a single midsummer harvest, using several grasses over a five-year period. The yield from single cuttings of the native *Andropogon furcatus, Panicum virgatum* and *Bouteloua curtipendula,* and of the pasture grasses *Bromus inermis* and *Poa pratensis,* increased from year to year as compared with the total yield from more frequent cuttings. The short grasses were more resistant to frequent mowing: the yields of *Bouteloua gracilis* from frequent and single mowings did not differ significantly, even in the fifth year, and those of *Buchloë dactyloides* only by the fifth year. The authors point out that in this true-prairie environment frequent mowing helped Buchloë by keeping the weeds down, whereas in the once-cut plots there was a gradual loss of Buchloë during the last three years because of shading by weeds and taller invading grasses. No effect of mowing was noted with *Elymus junceus.*

Cutting either once or four times during two growing seasons near Madison, Wisconsin, reduced numbers of *Andropogon gerardi* and *Panicum virgatum* and increased numbers of *A. scoparius* and *Bouteloua curtipendula* plants (Robocker and Miller, 1955). A photo taken in the next growing season shows height of the once-cut stand to be distinctly less than height of the control. On the same plots Neiland and Curtis (1956) observed that foliage height and production of foliage per unit basal area from clipped plants were reduced by a single midsummer clipping and roughly in proportion to degree of defoliation. Repeated removal of between 35 and 75 percent of the foliage reduced available carbohydrates in the crowns markedly.

Using row plantings of *Elymus junceus,* Thain (1954) found during a single year that production of tops and roots declined with frequency of clipping. Because of renewed growth, production of protein was increased with frequent clipping, but the amount of stored carbohydrates in roots and stem bases declined even more markedly than herbage and root production.

In the desert grassland of southern New Mexico, Canfield (1939) carried on a clipping experiment with *Bouteloua eriopoda* and *Hilaria mutica* over an 11-year period. All clipping treatments with Bouteloua proved too severe, even the lightest (end-season clip to two inches), partly because of wind erosion. On the other hand, frequent clipping to a four-inch height seemed to encourage Hilaria, a rhizomatous species growing in flooded depressions.

In the Intermountain West the response of *Agropyron spicatum* to defoliation has received considerable attention. Hanson and Stoddart (1940) showed that heavily grazed plants were smaller, produced fewer seeds and had markedly fewer roots which penetrated less deeply than ungrazed plants. Stoddart (1946) conducted a clipping study on this species in northern Utah for two years. The severe clipping treatments to heights of one and two inches, including fall clipping alone, reduced yield the second year and, except for very early spring and for fall clipping, caused heavy death losses. In Montana McIlvanie (1942) showed that repeated close clipping during the period of vegetative growth strongly reduced carbohydrate storage in the roots and stem bases of *A. spicatum*. In Montana, too, Heady (1950) concluded that clipping of *A. spicatum* once to six inches at the flowering stage was too severe a treatment to permit the plants to maintain themselves.

Blaisdell and Pechanec (1949), working on the Snake River Plains of eastern Idaho, showed that clipping *A. spicatum* to ground level at any date, except after dormancy in the fall, reduced leaf height, flower stalk production and herbage production the following year, in comparison with plants that had not been clipped at all. *Balsamorhiza sagittata* responded similarly but not quite so markedly: perhaps stored foods were less severely depleted in the heavy taproot of this forb. With both species, flower stalk production was the most sensitive criterion of injury. These results show very clearly the importance of season, which had been stressed by Stoddart: defoliations depress production most that are made when growth is well advanced in spring, root reserves are expended and substantial regrowth during the dry summer is impossible.

Driscoll (1957) clipped *Carex geyeri* for three years in eastern Oregon, removing 20, 40 and 60 percent of the forage during the summer. Although herbage production was not significantly affected, production of seed stalks was progressively reduced.

Working in the Wallowa Mountains of Oregon, Sampson (1914) concluded, although without presenting the evidence, that clipping *Festuca viridula* after the date of seed maturity—about September 1—did not damage the plants, and that flower stalks were produced fully as early, as uniformly, and as profusely on clipped plants as on plants that had remained unmolested.

Sampson and Malmsten (1926) observed that most of the clipping treatments they applied were harmful to *Agropyron trachycaulum* and *Bromus carinatus* in the mountains of central Utah. They came to the conclusion that early or frequent clipping was harmful to plants, but that late and infrequent clipping was not harmful and possibly beneficial. More elaborate studies (McCarty and Price, 1942) in the same locality, however, showed that both moderate grazing during summer and moderate grazing after seed maturity depressed the sugar and starch content of roots and stem bases in Bromus and Agropyron as compared with no grazing. Very early or very late single clippings depressed yields less than any other clipping treatments over a three-year period, but even these treatments depressed the storage of sugars and starches and the yields of herbage and flower stalks as compared with those of unclipped plants.

A clipping study on *Stipa pulchra* near Berkeley, California, by Sampson and McCarty (1930) included a 14-week winter period during which the plants were green but in which little height growth occurred. There appeared to be a slight reduction in total height growth from late clippings during this period, and this reduction may be significant, since it is consistent. The data suggest that progressively later harvesting, even in this winter period of slow growth, had progressively more effect in reducing carbohydrate storage.

In short, the results of all the clipping work on perennial herbs in this country may be summed up by Weinmann's (1948) experience in South Africa: "...It would appear that in most species of grasses any degree of herbage utilization will unavoidably result in some reduction in stored underground reserves".

Clipping the annual *Bromus tectorum* reduces yield, delays phenological development, and so diminishes the possibility for regeneration as the dry summer period is approached (Hulbert, 1955). Clipped plants of *Avena fatua* developed fewer leaves, and tillered later and less abundantly than unclipped plants (McCarty, 1935).

Using four California annuals, *Festuca megalura, Hordeum hystrix,* *Bromus mollis* and *Avena barbata* in row plantings, Laude *et al.* (1957) noted that repeated clippings stimulated tillering and delayed drying, even though the date of maturity of unclipped plants varied from May 21 for Festuca to July 6 for Avena. Early clipping stimulated tillering and seed production of *Bromus mollis* and *B. rubens* in most plantings but reduced seed production progressively during the latter two-thirds of the spring season. Their experiments suggested to these authors the possibility of reducing Festuca by grazing heavily early in the season, permitting the more desirable, later-maturing species to seed under lighter grazing pressure later. Burcham (1957) gives an example of the practicability of this suggestion in the field.

CLIPPING OF SHRUBS

In southern Utah Julander (1937) correlated shoot growth of aspen (*Populus tremuloides*) and cliffrose (*Cowania stansburiana*) with intensity of browsing by deer. Shoot production of aspen decreased strongly with intensity of browsing: only at the lightest browsing intensity (65-70 percent utilization of current year's growth) was there evidence of increased production over the four-year study interval. In contrast, shoot production of totally protected plants increased enormously. It must be remembered that this aspen reproduction on the Kaibab deer range had been overbrowsed for many years prior to the study, hence the very marked release under protection. Presumably the browsing of aspen root sprouts should be less damaging than the browsing of plants that are not supported partly by foliage which is out of reach of the animals, but clearly these root sprouts are very sensitive to clipping—much as lower branches of most shrubs and trees are.

Although the effect of light browsing on aspen cannot be evaluated from these data, that on Cowania can. It is interesting to note that moderate browsing (45-65 percent utilization) gave rise to greater total shoot length during the four-year period of study than either no or very heavy browsing. The author states that under moderate browsing, seed production appeared adequate for satisfactory reproduction.

Price (1941) evaluated the effect of 11 years of clipping *Cercocarpus montanus* and *Symphoricarpos oreophilus* in the fall in central Utah by total length of twigs produced in the twelfth year. The severe treatment, in which all current growth easily available to livestock was removed in September, reduced twig growth as compared with the unclipped controls. Leaving either one inch or two and one-half inches of each twig of Cercocarpus each year, however, gave greater production on all six of the bushes treated than on the unclipped controls. Similarly, leaving either two inches or two and one-half inches of Symphoricarpos twigs gave greater production in four of the six treated bushes as compared with the unclipped controls. From both, the length of twig removed averaged considerably more than 50 percent. It is not possible from the figures given to decide whether shrubs under the moderate or light degree of clipping were the more productive. Partly from other considerations, the author concludes that leaving one inch of the current twigs is a safe and practical degree of fall utilization for both shrubs.

In a four-year study of shrubs that had been ungrazed at least 13 years in central Utah and that produced many flowers but few twigs, Smith (1955) demonstrated a stimulative effect on vegetative growth of Cowania that increased with intensity of annual fall clipping. Another interesting effect noted by Smith was the persistence of an initial stimulus during four years. Two bushes of *Cercocarpus montanus* were severely pruned in the summer and fall of 1950, and two bushes of Cowania in the fall of the same year; no further treatment was applied. The pruned plants of Cercocarpus produced 44 times the total length of twigs of two comparable unpruned plants in 1951. The stimulus dropped sharply: in the succeeding three years the pruned plants produced 6.5, 1.7 and 2.6 times as much as the unpruned. The stimulus to Cowania was less marked: in the respective four years following treatment the pruned plants produced 3.0, 1.3, 1.3 and 1.3 times as much as the unpruned.

In northern Idaho over a six-year period Young and Payne (1948) studied the effect of clipping 50, 75 and 100 percent of the current twig growth on *Ceanothus sanguineus, Amelanchier alnifolia, Lonicera utahensis* and *Rosa jonesii.* As measured by total shoot production in relation to that of unclipped plants, Ceanothus was stimulated by both spring and fall clipping at 50, and perhaps 75, percent. Summer clipping was injurious at all intensities, however, and 100 percent removal was injurious at all seasons. The growth of Lonicera did not appear to be reduced appreciably by 50-percent clipping at any season or by 75-percent clipping in fall. In contrast with these species, shoot growth of Amelanchier and Rosa was reduced in relation to the controls in proportion to the intensity of clipping.

Garrison (1953), working in eastern Oregon and Washington, also found that species of shrubs differed in their response to clipping, although he concluded that "In general clipping stimulated twig production to the detriment of flower and fruit production". He removed 25, 50, 75 and 100 percent of the current growth each fall or winter from five shrubs for a four- and five-year period. The shrubs were *Purshia tridentata, Ceanothus velutinus, Chrysothamnus nauseosus, Holodiscus discolor* and *Cercocarpus ledifolius*. Unfortunately for our purpose, comparative yields are not given for unclipped plants. With Purshia there was some tendency to obtain greater twig yields from the two higher intensities of clipping. This was also true for Holodiscus and for Chrysothamnus at one site. Ceanothus, on the other hand, showed greater yields under the two lesser intensities of clipping. As in other clipping studies, the amount of variation in relation to treatment, which is partly attributable to differences in site, is considerable. It may well be doubted that the stimulative effects observed, particularly at heavy intensities of clipping, would persist if the treatment were carried on for a very long period.

SUMMARY OF EFFECTS OF HERBAGE REMOVAL

Generally speaking, the effect of grazing certain species in a community is to handicap those species and encourage others. Under range conditions, where the animals cannot be controlled as they are in pastures, the effect of selective grazing is commonly to reduce the proportion of palatable species. Some exceptions have been noted in which the quality of the vegetation has been improved by grazing; but in light of the number of examples to the contrary, these are truly exceptional. Obviously differences in palatability are not the whole explanation for trends under grazing: differences in growth form or phenology may also play an important part.

Successional trends are roughly proportional to grazing intensity: they are pronounced under severe grazing, and in some instances difficult to distinguish at light or moderate levels. Some observations suggest that palatable plants respond as favorably under light grazing as under no grazing, or as favorably under moderate as under light grazing (Nelson, 1934; Canfield, 1948; Hutchings and Stewart, 1953).

There is usually a doubt, however, as to whether the sampling intensity, comparability of areas being studied, or methods of measurement are adequate to make so fine a distinction. This doubt is strengthened by studies (Larson and Whitman, 1942; Johnson, 1956) that do show an appreciable effect of grazing at light intensities.

From this it follows that the exact composition of climax vegetation probably cannot be maintained by any intensity of grazing or selection of species other than those exerted by pristine wildlife. By itself this conclusion does not mean much. For one thing, grazing pressures of wildlife in prewhite days probably fluctuated, so that between variations in grazing and in other environmental factors, climax composition no doubt varied greatly. For another thing, we have no indication of magnitude. The difference between the composition of the pristine vegetation and the composition that can be attained under ideal management might be small or great, and it might well be greater in some plant types, or in some sites within a type, than in others. Too little is known about the effects of light or moderate grazing—that is, about trends under ideal management—as well as about character of pristine vegetation, to permit any very meaningful conclusion.

Although the number of studies bearing upon the effects of light herbage removals from individual grasses or forbs is not great, the weight of evidence points to a harmful effect. Reports that claim benefit to the plant from grazing are, for the most part, either speculative, crude in experimental design, inadequate in method, or cover so short a time as to reflect only the initial stimulation in herbage growth. The stimulation that occurs, which is usually measured in rapid leaf elongation, is evidently made at the expense of stored food reserves. Root growth is retarded and flower production may be reduced more than herbage growth.

It is clear that the physiological response to herbage removal needs much more investigation than it has had. Leopold's (1949) study indicates that removal of the growing point of grasses encourages tillering by lessening the production of auxin, but clipping in other studies, in which an appreciable volume of the herbage is destroyed, clearly inhibits tillering. What occurs in grazing would appear to be a resultant of two opposing tendencies. That interrelations between vegetative and reproductive growth may be involved is suggested by clipping studies that have been made with shrubs and by the experiments of Stapledon and Milton (1930), in which plucking of inflorescences, when they appeared, stimulated production of both tillers and roots.

The possibility needs to be investigated that cropping by grazing animals may have some, as yet unrecognized, beneficial effect on plants which clipping does not have. This possibility is suggested by the fact that what may have appeared to be moderate intensities of clipping as applied to grasses have generally been too severe for survival, whereas only the heavier clipping treatments applied to shrubs appear to have been damaging. Thus Holscher (1945) found that *Agropyron smithii* and *Bouteloua gracilis* declined under his most moderate clipping intensities, while the same species increased on the grazed range.

Light or moderate clipping stimulates many shrubs to greater vegetative growth than no clipping, and may continue to do this year after year. This growth appears to be made at the expense of energy that would otherwise be utilized by the plant in flower and seed production. Clipping of herbaceous plants, in contrast, retards vegetative as well as reproductive growth. Why should there be this difference? Perhaps the clipping of shrubs does not remove so great a proportion of photosynthetic material as the "same" intensity of clipping herbaceous species. For example, when 50 percent of the volume of a grass is removed, approximately 50 percent of the photosynthetic surface is taken away; but when 50 percent of the current twig growth of a shrub is removed, even on a weight basis, there may be leaves on spurs, or chlorophyll within the bark of older twigs, that can assist recovery. Another difference in treatment is that clipping studies with herbaceous vegetation have been made during the active growing season, whereas most observations on the harvesting of shrubs have been made when the season's growth has been completed. On the other hand, the carbohydrate reserves in herbaceous plants are stored in the stem bases or below ground, where they are practically inaccessible, whereas at least part of the reserves of shrubs are considered to be in the twigs where they are most easily removed by grazing.

The resistance of grasses to cropping is often extolled, usually with reference to the basal meristem as being an adaptation to grazing. The difference in their response suggests, however, that shrubs are more resistant to grazing than herbaceous plants. Under some circumstances, too, as where Blaisdell and Pechanec (1949) found a greater depression in growth from clipping *Agropyron spicatum* than *Balsa-*

morhiza sagittata, it appears that forbs may be more resistant than grasses.

THE QUESTION OF MULCH

Between consumption of plants as forage and fragmentation of plant residues by trampling, the amount of mulch or litter is not allowed to accumulate that would accumulate if there were no grazing. Because this effect is sometimes claimed as a means by which grazing benefits the range, we shall examine it in some detail.

Dyksterhuis and Schmutz (1947) described and classified the plant residues in the Fort Worth Prairie, distinguishing humic mulch, fresh mulch, cured herbage and green herbage. On range in excellent condition they found total organic matter above the ground surface, including green herbage, to vary from about 6,000 lbs. in April to 9,200 lbs. in September. Even at the height of the season's growth, green herbage made up less than half the organic matter above the ground. Comparable data on ranges in different degrees of condition are given for material collected April 10, 1945. At this time there were 9,037 lbs. of mulch per acre on relic grassland, and 5,321 lbs. on grazed range in excellent condition. In contrast there were only 1,938 lbs. on hay meadow, and 1,558 lbs. on range in fair condition. A notable fact was the very much greater and more uniform accumulation of earthworm casts under the litter of the undisturbed grassland than in the other areas.

Weaver and Rowland (1952) record even greater amounts of mulch on prairie than Dyksterhuis and Schmutz. They suggest that heavy mulch tends to promote a pure stand. Kelting's (1954) observation as to the diversification of species brought about by moderate grazing, in comparison with no grazing, supports this view. Also, in highly productive sites in the California foothills, a heavy accumulation of mulch encourages dominance by tall annual grasses at the expense of a more diversified assemblage of annual forage species (Talbot and Biswell, 1942). Clearing three years accumulation of mulch encouraged forbs at the expense of grasses, and this effect persisted during the following two years (Talbot *et al.,* 1939). Interestingly enough, the undesirable species that increased most greatly with heavy accumulation of mulch in the foothills of the Sierra Nevada, *Bromus rigidus,* did not show significant differences due to mulch treatment in Heady's (1956) studies in the Coast Range.

The implication of Weaver and Rowland's (1952) title is that accumulation of mulch can be "excessive" from the standpoint of welfare of the vegetation, and the authors offer four bits of evidence to support this view:

1. They obtained materially greater yields on unmulched than on mulched plots in 1951. This was an exceptionally wet year, with rainfall well distributed, and an advantage of mulch in dry years—moisture conservation—was at a minimum, while a disadvantage of mulch—low soil temperature—was at a maximum. Furthermore, the plants growing in the plots from which mulch had been cleared enjoyed the full benefit of the modification of surface soil by mulch during many prior years. In short, had the mulch been removed over a long period and had the comparison extended over dry as well as wet years, the results might have been materially different.

2. Weaver and Rowland cite the fact that Weaver and Tomanek (1951) in an adjacent pasture reported production in 1950 of 1.92 tons of herbage per acre from "good" as compared with only 1.53 tons from "excellent" condition range. In a similar comparison in 1949, however, Weaver and Tomanek measured approximately the same yield (1.58 and 1.60 tons, respectively), so the harmful effects of the accumulated debris could not have been very serious. Furthermore, this similarity of yield in 1949 makes the significance of the difference in 1950 doubtful.

3. Weaver and Rowland cite Dyksterhuis and Schmutz' (1947) data as showing that production in a prairie relic was lower than in mowed prairie. These data were gathered on April 10, 1945, before summer growth was well advanced, however, and the difference reflects only retardation of growth in early spring, a well-known effect of mulch, instead of lessening in total seasonal production.

4. In the loess hills of Nebraska Hopkins (1951) observed that removing mulch in the spring had the effect of increasing basal area of the vegetation threefold by the following autumn. This is cited by Weaver and Rowland, but they failed to include the significant statement made by Hopkins: "Yield was affected very little, if any."

It can be concluded that the evidence presented is hardly strong enough to support the claim. As evidence to the contrary, although admittedly not very strong evidence, Phillips (1936) shows greater production of *Andropogon scoparius* on relic areas than on mowed hayfields in central Oklahoma, and Schwan *et al.* (1949) increased production of *Poa pratensis* markedly in the ponderosa-pine type in Colorado by adding mulch. In the California annual type, herbage production increases as mulch increases (Bentley and Talbot, 1951; Heady, 1956). Removal of mulch by burning reduces yield of prairie vegetation (Aldous, 1934; Hanks and Anderson, 1957). However, this might be accounted for by the fact that, besides removing the mulch, burning may harm the plants directly.

Studies have shown that removal of mulch by burning or by clipping increases production of flower stalks of prairie vegetation (Burton, 1944; Curtis and Partch, 1950; Dix and Butler, 1954). The stimulation of early vegetative growth is attributed to more rapid warming of the soil upon removal of the heavy mulch blanket, and Curtis and Partch (1950) suggest that earlier growth in spring means more time for carbohydrate manufacture and storage before initiation of floral buds. Early growth is not necessarily advantageous to the plants, however, because in some situations premature growth could be damaged by frost. Stone (1951) concluded that the stimulative effect of fire on flowering of *Brodiaea ixioides,* a herb of the California chaparral, was due to the removal of overstory shade.

In western Kansas Tomanek and Albertson (1953) observed that production of flower stalks was less from ungrazed patches of *Andropogon gerardi* than from plants that had been grazed. This, following the experiments of Curtis and Partch (1950) with *A. gerardi* in Wisconsin, was attributed to the heavy mulch that had accumulated around the ungrazed plants.

Measurements have shown that under a mulch the soil is cooler than where it is bared and that soil moisture is maintained at a higher level during summer (Steiger, 1930; Weaver and Rowland, 1952; Hopkins, 1954). In an environment plagued by recurrent drought, like the prairie, this may well be the most important influence exerted by an accumulation of mulch, an influence that should enhance, not diminish, production.

For most of the western range the problem is not one of too much mulch but of too little. It is a problem of grazing so conservatively as to have enough cover from vegetation and litter to protect the soil from accelerated erosion and to provide a suitable microclimate for seedling establishment (Ellison, 1949a; Ellison *et al.,* 1951). This problem exists in a great variety of environments, from dry plains and deserts to humid montane herblands. The importance of mulch as well as of living vegetation lies in its encouragement of rapid infiltration of torrential rainfall that would otherwise erode the soil (Duley and Kelly, 1941; Beutner and Anderson, 1943; Packer, 1951; Hopkins, 1954; Hanks and Anderson, 1957).

The need for cover on the Plains, depending on the character of soil and whether the cause of erosion is wind or water, varies from 500 to 5,000 pounds of herbage per acre, standing vegetation and mulch combined (Osborn, 1956). In the mountains the needed cover has been shown to be about the same on a variety of soil types ranging from loose sandy loams to heavy clays—from 65 to 70 percent of the surface covered with vegetation and mulch, with the areas of bare soil small and dispersed (Ellison *et al.,* 1951; Packer, 1951, 1953; Marston, 1952; Ellison, 1954). On mountain rangelands the removal of herbage by heavy grazing is a major factor in accelerating soil erosion and deteriorating the site.

In sum, the evidence suggests that heavy accumulations of mulch tend to produce pure stands of grass, or at least to simplify the plant composition; to reduce numbers of shoots per unit area (Albertson *et al.,* 1957); and to reduce numbers of flower stalks; but whether they actually reduce herbage yield, as is often suggested, is open to question. Mulch has profound effects on microclimate above and below the soil line with corresponding influence on macro- and micro-organisms, about which little is yet known, affecting the processes of soil formation. Perhaps of most immediate practical importance to the maintenance of rangeland is the fact that mulch conditions the soil surface for rapid infiltration and protects it from erosion.

PLANT SUCCESSION AND SOIL EROSION

Because overgrazing has been the rule on rangeland, not only has plant composition been changed by grazing pressures but the vegetation has been thinned and in many instances destroyed. As a result of some degree of denudation, accelerated soil erosion is inseparably linked with overgrazing on arid lands the world over (Shantz, 1935; Jacks and Whyte, 1939).

If disturbance of plant cover occurred only occasionally, erosion would be less serious than it is. Repeated denudation, year after year, by whatever cause—plowing, burning, severe grazing, roadways, smelter fumes—makes accelerated erosion inevitable. Farming and fire may be least likely to denude the plant cover during dry years, but these are the very years when denudation by overgrazing is likely to be most pronounced. In arid lands fires may be rare because the fuel is eaten by grazing animals, denudation by plowing may be sporadic because of marginal returns and recurrent drought; but overgrazing, although causing less complete denudation in any one season, is important because it is widespread year after year. Its cumulative effects are attested by the rocky hillsides of semiarid parts of the world where overgrazing is centuries old, as in Mediterranean countries.

Unless soil erosion is very active, denudation of vegetation is followed by an orderly succession. The plants that first reclothe the surface usually either spring vegetatively from remnants left in the soil or are species whose fruits are adapted to be blown in by wind or carried in by animals. Abandonment of roads and farm lands in the Great Plains has given many opportunities to study such successions (e.g., Shantz, 1917; Costello, 1944). The following summary of five stages, typical of many successional sequences, is quoted from Costello:

> "Plant succession on abandoned fields in northeastern Colorado proceeds through the following stages: an initial stage characterized by *Salsola kali tenuifolia, Amaranthus retoflexus, Chenopodium album,* or other annuals; a forb stage consisting of a large variety of annual and perennial forbs and a few grasses; a short-lived, perennial grass stage in which *Schedonnardus paniculatus, Hordeum jubatum, Sporobolus cryptandrus,* or *Sitanion hystrix* are usually abundant; a stage marked by dense stands of *Aristida longiseta* or *A. purpurea;* and the fully developed mixed prairie association, consisting of a mixture of short-grasses, mid-grasses, forbs, and shrubs".

No doubt because many of the same weeds are abundant as a result of overgrazing, and because segments of the same sequences have been observed, especially on the Plains, it has been natural to divide secondary successions following denudation by grazing into four or five stages (Sampson, 1919). Implicit in this arrangement is the premise that the plant, or the assemblage of plants, is a reliable measure of its environment (Clements, 1928; Sampson, 1939), and thus an indicator of the degree of disturbance.

This relation is not always close when accelerated erosion is one of the environmental factors, however, and the customary conception of plant succession may not apply. The erosional process itself, or the specialized microhabitat of an eroded surface may nullify the reactions of vegetation on its environment, and in this case an orderly sequence of communities cannot occur. This fact can be appreciated only when it is recognized that exposed subsoils may present unique difficulties to plant establishment and survival. Graham (1942) may have sensed this in attempting to evaluate soil erosion as an ecological process. After noting certain anomalies in the colonization of eroded soils, he commented: "One cannot observe serious erosion, especially as it exists in the Appalachian Piedmont, without wondering if we do not need some adjustment of our theories about plant succession".

Trends involving accelerated erosion, being something distinct and apart from succession in any reasonable sense, have been distinguished as "destructive change" (Ellison, 1949b). The relations of vegetation to accelerated erosion no doubt vary with the degree of deterioration and the great variety of circumstances in which erosion occurs (Shantz, 1935). When soils are denuded of a plant cover and the friable topsoil has been lost, invading plants must cope with a very different environment than any provided in orderly succession. There is first the problem of the physical displacement of the seeds and young plants: simply maintaining a foothold may be difficult. Germination and survival are handicapped by a harsh microclimate at the soil surface, so that eroded spots, even though not subject to continuing displacement, may remain bare for long periods (Ellison, 1949a). Finally, eroded soils are notoriously low in productivity (Sinclair and Sampson, 1931; Voight, 1951; Joy *et al.,* 1954), and there is reason to believe that some eroded range soils may not be able to support enough vegetation to protect the surface until a residue of erosion pavement can supplement the plant cover (Ellison, 1954).

Because rangelands include such a variety of environments, the nature of normal geologic erosion differs greatly from place to place. One of the most urgent needs in range ecology is a clearer picture of soil-forming processes on rangelands and of the character of normal erosion, the better to reconstruct and evaluate accelerated erosion. For example, the existence of a deep soil mantle in subalpine environments is evidence of close control of the surface by vegetation for a very long time. Considering the steepness of slope that such a well-developed soil mantle may cover, and considering the frequency of torrential rainstorms in the subalpine zone, it is obvious that denudation of the soil for very long or on any extensive scale could not have occurred as part of the normal erosional process. By the same token, what surface washing may have occurred must have been both localized and occasional. The widespread evidence of destruction of such a soil mantle today, as shown by pedestalled plants or gullies (Ellison *et al.*, 1951), is obvious evidence of accelerated erosion. The distinction between normal and accelerated erosion in this example is easy because the anomaly is obvious, but on many ranges the soil mantle is less distinctive and the place of vegetation in formation and protection of the soil may be obscure.

OTHER EFFECTS OF HERBAGE REMOVAL

MICROCLIMATE AND SOIL MOISTURE

The effect of grazing, in both reducing standing herbage and accumulation of mulch, is to encourage evaporational loss and to create a lighter, warmer and drier microenvironment. Although the amount of rainfall intercepted by foliage and mulch on undisturbed prairie may be considerable (Clark, 1940; Weaver and Rowland, 1952), grazing does not appear to lessen interception sufficiently to offset the increased evaporation it causes from the surface soil. Thus grazing, or at any rate severe grazing, induces the physical conditions of the microenvironment associated with drought and permits invasion by weedy species. This is probably one reason why effects of drought and overgrazing are rather generally confused.

Steiger (1930) concluded that the general cover of vegetation in an upland true prairie reduced light to 20 percent of full sunlight or even more. Evaporation in midsummer was very much greater on clipped quadrats than in undisturbed prairie vegetation. Soil temperatures at depths of one, three and six inches were consistently higher, and soil-moisture percentages to depths of more than 12 inches were markedly lower in mowed than in undisturbed prairie. Because these differences in soil moisture are so great, they are probably significant and reflect the tendency for the surface to dry out if the protecting vegetation is removed. The presence of mulch contributes greatly to these effects on microclimate (Weaver and Rowland, 1952). Ellison (1949a) attributed the slow colonization of bare spaces in depleted subalpine herbland primarily to unfavorable microclimate.

Most comparisons indicate somewhat greater soil moisture under ungrazed vegetation than on grazed range (Lacey, 1942; Kelting, 1954; Lodge, 1954; Johnson, 1956). The differences are usually small, however, and for a reason to be discussed shortly, most of them are probably insignificant. It is only under severe clipping of herbaceous vegetation, as compared with the undisturbed, that very consistent differences in soil moisture have been recorded in the field (Clements *et al.,* 1929; Pearson, 1942). Reductions in transpirational loss from fairly severe clipping have also been observed with phytometers (Weaver, R. J., 1941, Pearson, 1942). Whether this reduction is due to reduced transpiring area or to diminished root volume, or both, is not apparent. A probable complication is accelerated transpirational loss per unit of leaf area associated with the abrupt reduction in proportion of tops to roots (Parker, J., 1949).

Unfortunately, for attempts to relate soil moisture to grazing, moisture content is usually expressed only as a percentage of dry weight of soil, which may not accurately reflect the amount of water in a unit volume under different degrees of soil compaction. An example, using Kelting's (1954) data from central Oklahoma, illustrates this point. Volume-weight determinations indicated that the soil of the grazed pasture was about one-third denser in the surface three inches than the soil of the ungrazed prairie. Kelting shows that percentage soil moisture in the zero to six-inch level was pretty consistently higher during the summer in tall-grass prairie than in the grazed pasture. Assuming the same volume weight for the full six inches, the pertinent figures for August 14, 1950, are:

	Prairie	Pasture
Percent moisture	15.5	13.0
Volume weight	0.9	1.2
Grams of soil in 1 cu. in.	14.748	19.665
Grams of water in 1 cu. in.	2.286	2.556

The percentage figures indicate more moisture in the prairie soil; but, because of the difference in volume weight, there may have been slightly more moisture in the pasture soil.

From these differences in volume weight it would appear that trampling by cattle, even at light or moderate grazing intensities, has an appreciable effect upon soil volume. No doubt this varies greatly with soil type. Hedrick (1948) found such variation in volume weight of the surface inch of soil under California annual vegetation that differences in compaction resulting from different intensities of grazing were not consistent. On the northern Plains, Lodge (1954) recorded significant differences in volume weight between soils of recently protected and heavily grazed areas on two of the four sites he studied, but not on the other two.

Daubenmire and Colwell (1942) compared two sites on a Ritzville silt loam in southeastern Washington, one of which had been protected from grazing for many years and the other heavily grazed. Soil-moisture percentages were consistently greater to a depth of a meter in the heavily grazed area. Volume weights of the two soils were not significantly different, which seems odd in view of two other differences. On the one hand, the soil of the protected area was much more strongly aggregated and had a markedly higher infiltration rate than the soil of the grazed area. On the other hand, and somewhat in contradiction, the surface soil of the protected area was more compact as measured by much less depression of the surface in forcing a steel cylinder into the ground. The differences in soil moisture would seem plausible because of more effective occupance of the site by the protected vegetation. The authors found markedly more plant material in the surface decimeter of soil of the grazed than of the protected area, which is attributable to dominance by the annuals and *Poa secunda* that replaced the native Agropyron. There were markedly more bacteria, actinomyces and molds in the surface decimeter of the grazed than of the protected area, which probably reflects this greater amount of organic matter.

INCIDENCE OF FIRE

Removal of fuel by grazing must be reckoned a factor in reducing the incidence of fires. References have been cited to suggest that fires in prewhite days may have kept cactus, scrub oaks, mesquite and juniper from invading grassland, but it is important to note that direct evidence of the efficacy of fire is meager. The effectiveness of fire varies, of course, with species of woody plant and with the abundance or scarcity of fuel. In the Southwest fire appears to be effective in destroying the half shrubs Aplopappus and Guitierrezia—the woody plants most susceptible to control by the competition of herbaceous vegetation—fairly effective in destroying cacti, but essentially ineffective in destroying mesquite (Glendening and Paulsen, 1955; Reynolds and Bohning, 1956). Humphrey (1949) differs from these authors in believing, from the study of two burns in southern Arizona, that fire is fairly effective against mesquite.

Hatton (1920) attempted to appraise the effects of grazing on the incidence of fires on western national forests and concluded that "normal" grazing—"grazing only to such an extent that the forage crop does not decrease from year to year"—was distinctly advantageous in lessening fires, both by removal of the herbaceous undergrowth and by hastening the decay of litter through trampling. What was considered "normal" grazing between 1900 and 1919 would probably be considered overgrazing today. Pearson (1950) also expressed the view that in ponderosa pine forests of the Southwest, grazing bunchgrasses to a height of six inches would reduce the fire hazard without danger of soil erosion. Talbot (1937) considers this degree of utilization excessive, however.

Ingram (1931) made a significant point that grazing would not automatically reduce the fire hazard if unpalatable but more flammable species were to increase. His three-year study provided an example in that bracken (*Pteris aquilina*) decreased an average of six percent on ungrazed plots, but increased 20 percent on grazed plots.

With time the viewpoint changes. Today, considering the western range as a whole, it would appear that fire is a lesser scourge than overgrazing. For reasons that have been outlined above, far more accelerated soil erosion, both in the form of sudden mud-rock floods and in the persistent gnawing away of the surface soil from numberless slopes, takes place because of overgrazing than because of fire.

EFFECTS ON OTHER ANIMALS

The effects of grazing on the faunal part of the biotic community are more difficult to evaluate than on the vegetal part principally because of the difficulties of sampling mobile animal populations. At any rate, few studies have been made of the effects of livestock grazing on other animals.

Attention has already been called to the observation by Dyksterhuis and Schmutz (1947) that a remarkably deep and continuous layer of earthworm casts occurred beneath an undisturbed prairie mulch. Such a continuous layer was absent beneath the considerable mulches that had been developed on grazed range. In want of much information on the effects of grazing on animal life in the soil, this observation suggests, at least, that the effects may be profound.

One of the best known effects of overgrazing on insects is an increase in numbers of grasshoppers (Weese, 1939; Smith, 1940a, 1940b; Clark, 1948). Smith's studies indicate that grasshoppers are more numerous on range in depleted than in good condition, or in midseral stages of secondary succession after land is abandoned, but that when the cover is reduced so greatly that erosion becomes marked, numbers of grasshoppers decline. In contrast to grasshoppers, beetles, particularly Chrysomelids, tend to decline progressively with declining status in range condition or succession. The interrelations between numbers of species, numbers of individuals, and habitat change is extremely complex. Actually, it is a gross oversimplification to consider a taxonomic grouping, like the grasshoppers, as an ecological unit. The food habits and microenvironmental requirements of different kinds of grasshopper have been shown to be highly specific (Isely, 1946; Anderson and Wright, 1952). One kind of grasshopper may feed on a particular species of plant exclusively; another kind selects another species; some kinds have somewhat broader tastes; and still others are omnivorous.

A controlled greenhouse experiment demonstrated that bluegrass (*Poa pratensis*), weakened by frequent clipping, was much more subject to injury from white grubs (*Phyllophaga sp.*) than bluegrass less frequently clipped (Graber *et al.,* 1931). This experiment corroborated earlier observations in Wisconsin pastures in which damage to bluegrass from white grubs was correlated with deficient root and rhizome development resulting from deficient fertility, thin soil or severe grazing.

On the other hand, the reviewer once observed in a mountain meadow in eastern Idaho that most of the *Festuca idahoensis* plants inside a ten-acre, four-year-old cattle enclosure were dead, while the plants on the closely grazed outside range were alive and fairly vigorous. The standing bunches of dead grass could be lifted easily, and at the base of each the root crown had been eaten out by larvae that looked like large cutworms. Possibly this small area of standing, cured grass had been attractive to the egg-laying adult insect; at any rate, in this instance it appeared as if the cattle had performed a useful service to the outside grass plants by keeping their tops grazed down.

Smith (1940a, 1940b) noted that meadowlarks (Sturnella) tended to be most abundant in the midseral stages of prairie succession, which he attributed partly to the abundance of grasshoppers in these stages.

The reciprocal relations between the effects of rodents and rabbits upon the range, and of range condition on the abundance of small mammals, vary greatly with circumstances. They vary with species of animals, with vegetation types, with kind of topography and soil, with range condition and probably with associated species of animals. A mere outline of these complex relations, which have been reviewed in more detail by Bond (1945) and Kalmbach (1948), will be attempted here.

Small mammals harvest vegetation and thus compete in some degree with domestic livestock. The degree of competition is probably most severe, as it is between big game and livestock, on depleted range. Competition is offset in some measure by the fact that different grazing animals often prefer different food plants. Where this is true, rodents and rabbits may exert pressure against plant species low in the successional scale, and thus tend to encourage species that may be palatable to larger grazing animals. Thus rodents and rabbits can hold a depleted range in depleted condition indefinitely or deplete it further (Norris, 1950; Moore and Reid, 1951), or they can exert pressure to advance succession (Bond, 1945).

Rabbits and rodents may disseminate and even plant the seed of undesirable species such as cactus, juniper and mesquite (Cook, 1942; Wolff, 1948; Glendening and Paulsen, 1955). On the other hand, they may also destroy large numbers of seeds of undesirable species by consuming them and by grazing the young plants. Rodents may also plant or destroy the seed of desirable species, for example, *Purshia tridentata* (Hormay, 1943).

Burrowing rodents have constructive as well as destructive influences on the soil. Their constructive influences in promoting soil development is difficult to assess, but their destructive influence in speeding up erosion is well known. Pocket gophers (Thomomys) and ground squirrels (Citellus) have received most attention in this respect. Several writers (Day, 1931; Gabrielson, 1938; Howard, 1953) indict these rodents as a principal cause of accelerated erosion on the western range. However, conceding that burrowing rodents are agents in geologic normal as well as accelerated erosion, there is reason to think that the amount of accelerated soil loss they cause is directly related to degree of range depletion from overgrazing (Ellison, 1946; Longhurst, 1957). It is widespread thinning of the plant cover by close grazing and trampling, and consequent soil exposure, that lessens infiltration and encourages overland flow, the immediate cause of erosion.

There has been a sort of successional trend in thought with regard to range rodents. The earliest attitude, probably influenced by the distorting effects of extreme livestock overgrazing on the range, is that rodents are evil in and of themselves, and fit subjects only for extermination. A later concept is that of large numbers of rodents as "animal weeds" which are not so much a cause of range depletion as a symptom of some kind of disturbance, usually overgrazing. An outgrowth of this concept is that rodents may exert pressures on the range in almost any direction, depending upon circumstances. They can have either constructive or destructive influences, or both, upon vegetation and soil. Most biologists seem to believe that normally their net influence is constructive and that their destructive influence is magnified by improper land use.

Overgrazing by livestock, because it has encouraged the spread of shrubs into grassland, has had the effect of increasing deer habitat in some places, and therefore is thought to be one of the factors causing the overpopulations of deer that exist in some parts of the West (Leopold, 1950). There are of course distinct competitive relations between deer or pronghorn antelope and sheep, and between elk and cattle; and overgrazing by one class of animal is often disadvantageous to another. In southern Texas, antelope are said to prosper on overgrazed cattle range because of the dominance of forbs. These forbs are not the ones of the climax vegetation that antelope prefer: their importance derives from their abundance, not their palatability. On the other hand, invasion of shrubs has been a disadvantage to antelope, and there is little forage for antelope on overgrazed sheep range because the two animals tend to eat the same forage species (Buechner, 1950).

DISCUSSION AND SUMMARY

Succession is commonly thought of as a constructive process: the origins of the word suggest growth and progress. In primary succession the development of soil with its contained organisms, including the complex vegetation it supports, is certainly a constructive process. Most of the familiar forms of secondary succession are also constructive in character. Examples that come to mind are the communities that succeed one another after fire or after abandonment of plowed land.

In contrast, secondary successions resulting from grazing are commonly thought of as being other than constructive. There are enough examples of severe overgrazing of range vegetation so that everyone who has been interested in the matter at all knows that reduction of plant cover by overgrazing leads to accelerated soil erosion by wind or water. Even though grazing changes the character of the vegetation without reducing cover sufficiently to cause erosion, the change is usually toward a vegetation that is less palatable to the grazing animal and somewhat less productive.

The negative character of change associated with grazing is suggested by the term "retrogression", advocated by Sampson (1919). Unfortunately, this term, as Sampson used it, has two serious weaknesses. First, it includes trends involving accelerated soil erosion that are not successional at all. Accelerated soil loss is nothing more nor less than destruction of the site, and trends involving accelerated soil erosion are more properly distinguished as "destructive change" (Ellison, 1949b). Second, the term grows out of confusion between primary and secondary succession, in which changes in the course of "retrogression" are presumed to retrace in reverse order changes involved in the original development of vegetation and soil. In the specific area to which the term was initially applied, at least, progression and retrogression up and down the same scale do not occur. Changes in vegetation may proceed in several directions, depending on the character of grazing pressure applied. The term "retrogression" would be very useful if it could be stripped of these connotations to mean trend away from the original undisturbed character of the vegetation with the protective relation of vegetation to soil unimpaired.

Various benefits conferred by grazing animals on vegetation have been suggested, and we can summarize the principal ideas developed in the foregoing review by considering each presumed benefit in turn:

1. Cropping may stimulate herbage production. The most clear-cut evidence of stimulation is that of twig production of shrubs, although to the detriment of flower and fruit production. With herbaceous vegetation harvesting the foliage generally results in lowered root reserves and production of flowers, herbage and roots. Height growth of leaves may be stimulated, but such stimulation is short lived. The bulk of the evidence, under laboratory conditions or in the field, is that harvesting of photosynthetic tissue is harmful to the plant. The evidence, it is true, is mostly derived from severe defoliation which may well give a biased indication of the influence of grazing in nature.

2. Grazing may help a plant endure drought by reducing the area

of its transpiring surface. The thought here is that a better moisture balance is established between roots and crown. Actually, grazing appears to harm roots, probably because stimulated top growth is made at their expense. Up to now this hypothesis lacks experimental support.

3. Grazing, by removing some of the herbage, lessens the amount of mulch and thus, by encouraging early spring growth, increases production. The detrimental effect of excessive mulch, while frequently suggested, has not been clearly demonstrated. On most rangeland the problem is one of getting enough cover from mulch and from living vegetation to protect the soil adequately under grazing. The intensity of allowable grazing over much of the western range is basically to be determined by whether enough herbage is left, partly in the form of mulch cover between plants, to protect the soil. Trampling helps break up mulch, too, but it is doubtful that this benefits the vegetation.

4. Grazing animals carry the seeds of forage species from place to place. That grazing animals transport seeds, both externally and internally, is well known (Müller, 1956). So far as external transport is concerned, the fruits of undesirable species are at least as well adapted as those of desirable species; so this could hardly be a means to encourage dominance by desirable at the expense of undesirable species.

With regard to internal transport, Müller points out that it is from species most eaten that most seeds are ingested and distributed in dung, and Major (1957) suggests this as a compensation for the disadvantage of high palatability. This hypothesis is attractive because it alone explains the advantage of palatability to the plant. The fact is, however, that very few forage plants appear well adapted for this kind of dispersal. Many of them have large, soft, late-developing fruits that shatter easily and fall to the ground. The persistent fruits and small, hard-coated seeds of some clovers are a conspicuous exception. A case for this hypothesis can also be made with the annual, *Chenopodium album,* the seeds of which were among the most numerous found by Müller in the dung of domestic and wild animals in the Swiss Alps. When the seeds of Chenopodium are ripe, its life cycle is essentially over, and no harm can come to the plant itself from being grazed—a compensation not shared by perennial species. On the other hand, Chenopodium is also palatable when it is immature, and the advantage of seed dispersal would not be gained when it is grazed at this stage. Furthermore, despite its palatability, this species is an indicator of severe disturbance, not of some advanced degree of succession. In short, the hypothesis helps explain the distribution of some species, and perhaps an occasional fruit of every palatable species is transported by animals in this way, but it may well be doubted that this slender advantage of palatability is of sufficient value to many plant species to offset its obvious disadvantage.

5. Trampling helps plant seeds of forage species. This claim, frequently made, does not appear to be supported by carefully designed experiment. The advantage of such planting would be most clear-cut on denuded surfaces where some amelioration of a harsh microclimate by soil covering is necessary. It is doubtful that artificial help of this kind would be needed where the surface soil is of unimpaired structure and a normal cover of mulch and vegetation overshadows the surface.

6. Livestock trails, which tend to follow the contour, check the overland flow of water and thus encourage infiltration. Admittedly, livestock trails may do this. The proper place for water to sink into the soil, however, is where the raindrops fall, not some inches or feet away after it has run over the surface. The existence of well-defined trails suggests excessive grazing use, which use is usually responsible for the low infiltration capacity of the soil at the point of raindrop impact.

7. Grazing animals, by their excrement and decay of their bodies, fertilize the range. No doubt this is true, but they cannot add more elements to the soil than they get from the plants they eat; so this does not seem to be a very real benefit. It is quite possible, however, that animals could distribute a fertilizer that might otherwise be highly localized—for example, a trace element important to plant growth that might be directly available only to the plants of certain localities. It has been suggested (Carpenter, 1940) that hormones in the urine of mammals may stimulate plant growth, but no evidence is given.

One cannot be very greatly impressed, after examining this catalog of presumed contributions of grazing animals to the welfare of range vegetation, by the supporting evidence. Certainly nothing in the mechanics of grazing provides so clear an explanation for range improvement as the simple mechanics of selective grazing to the opposite effect. The benefits of grazing, if any, would appear to accrue to the ecosystem, to the range as a whole, instead of to the palatable species of plants that are grazed most. One frankly conjectural possibility in this category that has not been mentioned is that, by creating areas of disturbance, grazing animals provide a more varied environment and thus maintain a more complex flora than would otherwise occur. This reservoir of disturbance-species, or variant genetic material, might be useful to the ecosystem in maintaining a plant cover during times of stress, such as during periods of climatic change.

In spite of the flimsiness of all these arguments, the fact is that ranges do improve under grazing, albeit from conditions of depletion. An example, which has been analyzed elsewhere (Ellison, 1958), is given in some desert-shrub data presented by Hutchings (1952). The vegetation on two sides of a fence is compared over a 19-year period, 1934 to 1952. For the sake of illustration we shall consider the production of only *Artemisia nova* and *Chrysothamnus stenophyllus,* two species of very different palatability. Under managed grazing about two-thirds of the current growth of Artemisia is eaten by sheep each winter and only about one-tenth of that of Chrysothamnus. Despite this apparent handicap, production of Artemisia increased from seven to 44 percent of the total; while under continued heavy grazing production declined to four percent. In contrast, production of Chrysothamnus under managed grazing declined from 23 to five percent and increased under heavy grazing to 33 percent of the total.

Here a palatable species, handicapped as it may be by selective grazing, has increased at the expense of a less palatable species. Most examples of range improvement under grazing, although different species are involved, pose the same paradox. How can such trends occur?

A clue in our desert-shrub example is provided by the behavior of *Salsola kali.* This introduced annual is consistently more abundant on the heavily grazed range, and in years of abundant early summer rainfall it may be widely conspicuous. On range in good condition Salsola plants of any size are observed only on disturbed spots, like areas around rodent dens. Because they permit Salsola to flourish—to the point in some years of making up a high proportion of the herbage—it would appear that the perennial species dominating the heavily grazed range in our example are not very efficient in utilizing the resources of their environment. This is to say, Chrysothamnus is less well adapted to this environment than the more palatable Artemisia.

We need not concern ourselves here with the question as to what the specific differences in adaptability of the two species may be. Superficially, at least, it appears to be a matter of drought-resistance. Many dead plants of Chrysothamnus are to be found, even on the heavily grazed range, apparently killed by recent drought. Artemisia, on the other hand, while its growth was reduced in drought years, was not killed outright and, judging by the relative scarcity of Salsola on the managed range, was able to utilize more of the moisture that fell. Thus—at the risk of oversimplification—if drought, competition and the handicap of grazing are taken together, Artemisia is able to flourish so long as grazing pressure is restricted; but if grazing pressure is increased greatly, Artemesia is suppressed and the less well-adapted Chrysothamnus is given the advantage.

A successional trend with a probably similar cause has been reported from the Big Horn Basin in Wyoming (Cooper, 1953). Here most of the grazing is done during the growing season rather than, as in the previous example, during the dormant period. After eight years of different grazing treatments—including deferment in some years and generally lessened grazing intensities—range dominated by *Artemisia tridentata* lost most of its brush and was taken over by grasses, mainly *Agropyron smithii* and *A. spicatum.* That these very striking changes occurred within so short a time suggests that the pristine vegetation of the area was grassland, not shrubland, and that sagebrush is an invader whose position of dominance is maintained only so long as the grasses are suppressed by overgrazing.

It is believed that the evolution of modern grazing animals coincided with the evolution of grasses (Taylor, 1949). That the evolution of grazing animals was dependent on the development of aridity and grasslands is perhaps obvious, but in such matters the ecologist may reasonably expect some evidence of mutual dependence. One of the principal purposes of this review has been to discover such evidence. The most that can be said, however, is that the evidence of grazed plants' dependence on grazing animals is rather negative: the relation appears to be essentially one of parasitism by the animals. The fact that, under the apparent handicap of millennia of grazing, most of the dominant species of the world's herblands are palatable plants, not only to buffalo and elk but to domestic livestock, is very impressive indeed. It suggests both that the adaptive process in evolution is exceedingly complex and that perhaps we have been unable to discover a dependence of plants on grazing animals which is real and important.

This is certainly to be reckoned one of the notable paradoxes of nature. Thus, in spite of all our study and thought, from the observations of herdsmen before Abraham's time to the results of scientifically designed experiments in the present day, we have very little real comprehension of what is perhaps one of nature's simpler mysteries.

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