

ECOLOGICAL PRINCIPLES IN RANGE EVALUATION¹

E. J. DYKSTERHUIS

*U.S.D.A., Soil Conservation Service
Room 604, 134 So. 12th, Lincoln 8, Nebraska*

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INTRODUCTION

Range ecology has certain unique features, but its fundamentals are those of all ecology. Thus, current perspective in range evaluation was expressed more than 30 years ago by the marine ecologist who postulated: If the problem covers enormous numbers of organisms, or a large extent of space, or a long period of time, the effect of minor factors is so deeply submerged that we are not able to trace them. The greater the magnitude of the problem the fewer the factors which need to be considered in its analysis, and the less complex the terms of its solution (Allen, '26).

For our purpose the term "range evaluation" will be used to mean accurately estimating the amount, quality or worth of range. Range will mean only native pasture on natural grazing land. Ranges generally are extensive areas producing little per acre in comparison with tame pastures. Moreover, ranges have far greater

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heterogeneity in soil and in vegetation, within units of practical size for appraisal and management, than do tame pastures.

One reason for evaluating ranges is direct interest in probable production of animal products over a term of years. Results from research as well as practical experience are expressed in terms of weight gains by animals of named size and age. Factors commonly considered are: (a) kind of forage produced on the pasture, (b) weight of the forage consumed per unit of area, (c) nutritional balance of consumed forage, (d) efficiency of the animals in converting the forage to animal products, and (e) effects of any soil amendments or animal feed supplements.

There is another related but different area of interest in range evaluation; it is the one to be considered here. Its devotees concern themselves with the fundamental reasons for differences in yields of different ranges or of the same range at different times. The primary concern is with average current yield and average potential yield. Moreover, yield predictions regularly imply yields without deterioration of site or cover. Such yields are commonly expressed in terms of weight of foliage produced per unit of area or in terms of numbers of specific kinds and classes of grazing animals that safely may be grazed for given seasons. In contrast with the first area of interest, factors commonly considered are: (a) climate, (b) soil, (c) quantitative relations in the current vegetation, and (d) past degenerative or possible future successional changes as viewed from a norm, potential or climax plant cover for the physical environment. When men of both areas of interest are shown a range together, those of the first group may ask "What have we here?", while those of the second group should ask "What is happening here?".

Difference in yield and hence worth of different ranges is unquestionably associated with difference in vegetation. The earliest attempts to inventory range resources dealt almost exclusively with differences in vegetation. In the western United States this resulted ultimately in a classification of ranges comprised of 18 standard vegetation or grazing types (Stoddart and Smith, '55). Subtypes, based on dominant species encountered locally, were recognized, and grazing capacities were assigned on the basis of coverage by different species in each subtype. The system was used on Federal grazing lands for over 30 years and into the present decade. Soil

differences and the successional position of the vegetation were not mapped or included in the computations. The science of ecology was young and little used in resource inventories.

In 1916 F. E. Clements, with his Carnegie publication "Plant Succession", first organized the field of dynamic ecology as a unified science (Cooper, '26). Shortly thereafter, plant succession in relation to range management received monographic treatment by A. W. Sampson ('19). How both earlier and later research and experience increasingly influenced rangemen, until synecology became the foundation for a range evaluation procedure, has been reviewed elsewhere (Renner, '48; Dyksterhuis, '49).

PROBLEMS

Range evaluation inevitably entails making or using land surveys, mapping of environmental and vegetative features, and determination of acreages. If quadrats or animal products are measured, the results are only small samples from a vast array of different kinds of land with different kinds of vegetation that varies greatly from year to year under influence of both grazing and weather. Moreover, data gathered must be such that their conversion to or expression in economic terms is possible (Burdick, '57).

It will be well to remember that boundaries of range pastures seldom coincide with boundaries of soils and natural plant communities. Therefore, management seldom can be accurately adjusted to differences in soil and vegetation. Only major differences within a pasture have practical import because the pasture becomes essentially the unit of management when the gate is closed behind a certain number of animals. Units mapped, and data concerning each gathered in range evaluation, must be justified, considering value per acre and economical management.

Ecologists accustomed only to detailed analyses of small tracts find it difficult to make this necessary adjustment in thought and methods. Those who would apply ecological principles in range evaluation must think also in terms of application on millions of acres; entire Soil Conservation Districts, National Forests, Taylor Grazing Districts or Indian Reservations, if not states and regions. Some ecologists may be dismayed by the rangeman's willingness to generalize and base conclusions on information too sketchy for scientific publication but obtained over vast areas. So, too, the

field technician is sometimes dismayed by the researcher's or the professor's generalizations concerning range, based on admittedly careful measurements of habitat factors and vegetation, often through decades, but on only a few small tracts attached to or near the university or the experiment station. Theories and principles in synecology are best formulated by those in scholarly pursuits, but field technicians are best able to test them for the necessary universal application. Technicians observe and compare a vastly greater number of communities and environments, at all seasons, and with more knowledge of past land use. Since both types of experience are seldom realized in one lifetime, we have much to learn from each other.

The science of ecology has long pointed to correlations between physical environment and natural vegetation. But much range vegetation is quite unnatural, reflecting mainly its history of grazing. Grazing influences received but little attention from synecologists until quite recently. Consequently, rangemen who attempted to interpret range landscapes in terms of published synecological data often have floundered, but no more so than research ecologists working in range areas who evidently assumed that ranges supported natural vegetation simply because they remained uncultivated. I say "evidently" because correlations between the physical factors of ranges and their vegetation often are reported without mention of grazing; much less, degree of grazing disturbance.

The foregoing problems and special needs, when applying ecology to range evaluation, have focused the interest of many rangemen on certain ecological principles that are believed to be generally applicable. Principles to be discussed are those of the ecosystem, continua, aggregation and community, stratification and periodicity, and succession and climax. Since few principles can be attributed to any one person, citation is difficult. Also, phrases and sentences from different authors may be spliced to better express a principle in a particular setting. In this case, much has been taken from textbooks by Clements and Shelford ('39), Dice ('52), Odum ('53), Woodbury ('54) and Oosting ('56), and from monographs on theory by Cain ('44, '47), Tansley ('35) and Whittaker ('53).

THE ECOSYSTEM

The first principle to be recognized is that range is an ecosystem, involving the accumulation, circulation and transformation of energy and matter through such biological processes as photosynthesis, herbivory and decomposition, with the non-living part involving evaporation, precipitation, erosion and deposition, reacting to the living part, and with coactions between organisms. No ecosystem is closed to influences producing gradual change. Yet, it may be granted that sustained and normal functioning should be implied in the term.

Tansley ('35) noted that the tendency to evolve dynamic equilibria is familiar in all sciences. The degree of perfection of a range ecosystem is measured by relative stability of the equilibrium between climate, vegetation and soil. Range animals are regarded as influents. Natural vegetation in equilibrium with an unmodified mature, normal or zonal soil is more stable than natural vegetation developmentally in equilibrium with an immature soil, but the latter, too, is here regarded as an ecosystem. This conforms with a polyclimax viewpoint. On the other hand, only an incipient ecosystem exists where natural vegetation is partially or wholly destroyed and secondary plant succession is operative in restoring equilibrium with the degree of soil development.

The term "anthropogenic ecosystem" was proposed by Tansley ('35) for great stability of vegetation under cultural treatments by man. Forest converted to grassland by grazing animals was suggested as an example. But to rangemen of the United States this example is more likely to call to mind instances of accelerated erosion and encroachment of unpalatable woody plants than it is likely to suggest stable soil and cover. On steep non-arable lands the cultural treatments necessary to maintain an unnatural cover have seldom been feasible economically.

While the principle is accepted that man and his grazing animals *must* be intergrated into the range ecosystem, yet a range ecosystem, in the sense of stable native pasture cover on natural grazing land, should not be confounded with the forest ecosystem of natural forest land. Principles governing classification of range vegetation should be such that at basic levels they also segregate range lands from forest and other lands. Daubenmire ('52), in considering forest vegetation of the Rocky Mountains, was concerned with an

approach to vegetation classification that might apply effectively in this complex region as well as elsewhere. He concluded with others that: "We should look upon complex ecosystems as the natural units, and that macroscopic vegetation in its entirety comprises the best criterion of ecosystem".

Evans ('56) emphasized the need to specify the level on which an ecosystem is being studied. Wonderfully complex interactions are entailed at many levels. In range evaluation we examine at the level of natural types of plant communities and their environments, both sufficiently extensive to be shown on common land survey maps.

To quote Odum ('53), "The ecosystem rather than the community, is the real basic unit. Therefore, there is no logical reason why a community cannot be named after some non-living community habitat feature . . .". Moreover, he concluded that the number of community units to be recognized depends on practical considerations, that names must be meaningful but short or they will not be used, and that the best way to name a community includes picking stable features, whether living or not. Similar conclusions have been reached in range evaluation (Dyksterhuis, '49, '52) excepting only that names of units of the range ecosystem should perhaps regularly denote non-living features.

The name "sagebrush community", denoting a living feature, may be used as an example to point up objectionable features of such names. In range evaluation we must, I believe, regard sagebrush as a conspicuous feature of many quite different environments. In some it is simply and wholly an invader because of overgrazing. From these it is excluded in the relatively stable condition of the ecosystem (Cooper, '53). In other environments it is a normal component of stable ecosystem units but in different amounts. On these it may be reduced by chemicals or otherwise, but the non-living part of the ecosystem remains essentially unchanged, and sagebrush should be expected to return in former amounts unassisted but ultimately limited by competition of other members of the community as equilibrium is restored.

In range inventory procedure of the Soil Conservation Service, local names, for example, "mesquite flats", "saltgrass bottoms", "sagebrush type" and "buckbrush coulee", were replaced, understandably with opposition, because we believed such names posi-

tively misleading and unscientific. They misled because they implied a necessary or natural relation between certain invading plants and certain kinds of land. The plant by which the kind of place had come to be known was more often than not simply an indicator of overgrazing instead of a permanent feature of the ecosystem-unit.

Uncultivated range lands long protected from grazing and with relatively stable vegetation are used to determine practical subdivisions and suitable names for units of the ecosystem. In developing this classification of abstract units we still may say with Clements ('35): "The natural plant communities are not merely the best integrators of the effects of climate and soil, but axiomatically they are also by far the best judges of these two complexes in terms of plant production". The units of the physical environment that are mappable and that also subtend a significant difference in kind or amount of climax vegetation are termed "range sites".

Plant communities may be visualized either in terms of a specific stand or in the abstract from several concrete examples of stands (Nichols, '23; Oosting, '56). So, too, the term "range site" or "site" is commonly used as an abstraction to avoid constant repetition of such phraseology as "type of range site" or "habitat-type". We refer, for example, to "Choppy Sandhills, 15 to 19 inches precipitation belt, Nebraska" as a range site. Different portions of such a site are occupied by different plant communities in response to different grazing treatments. Stable (climax) community composition of each site, expressed as relative coverage or annual growth by species, becomes our measure of potential productivity.

Productivity of an ecosystem, as described by Odum ('53), may be briefly restated for purposes of range evaluation as: the *rate* at which energy can be stored by photosynthesis of producer organisms in the form of organic substances which can be used as food materials by consumer organisms. Departures from this potential type of vegetation for a site can be quantified as relative departures in mass produced annually, from potential downward along a gradient of community degeneration.

Decline in forage production and decline in productivity of a range site are not strictly parallel but there is a direct relation.

The relation might be parallel as well as direct were it not for almost ungrazable species that increase or invade, filling the voids left by the most grazed species. Thus forage production may decline more than foliage production. But ordinarily the taller, higher producing grasses are replaced by shorter, lower producing species because the latter escape grazing of too high a percentage of their photosynthesizing tissue. With rest from grazing the taller grasses can again utilize their competitive advantages and tend to restore potential productivity.

Clements and Shelford ('39) emphasized that habitat should mean only the physical and chemical factors that operate upon the community. The term "range site" is used here with the same connotation. Hence biotic factors are not considered to be site factors. Moreover, this approach is not the "habitat approach" as described among seven approaches to ecology by Woodbury ('54). The habitat approach has commonly dealt only with current environment and current inhabitants. In the ecosystem approach such knowledge is only a beginning because the same site can support biological processes at various rates corresponding with various degrees of imbalance between the living and non-living parts of the system. Contrasts in the native vegetation on opposite sides of range fences show such differences in almost every township of the range country. In almost every county there are areas undisturbed by cultivation, grazing and mowing where the vegetation is relatively stable, providing the best available places for study of ecosystem units and their relation to sites.

In the course of studying many such protected areas, judgment must be made on how many types of sites it will be meaningful to recognize for range evaluation in a specific region.

CONTINUA WITH MEASUREABLE GRADIENTS

The second principle is largely derived from wording in the *Soil Survey Manual* of the U.S.D.A. ('51). The statement there describing soil as a continuum has been extended and modified to include climate and vegetation.

Climates, plant communities and soils tend to cover the earth as a continuum with measurable horizontal gradients. A climate, a plant community or a soil, in the sense of an individual, is normally a dynamic three-dimensional section of the landscape with a

range in characteristics or a modal set of characteristics set by our logic, not by nature. Asa Gray long ago observed that species, too, are man-made, not separate creations. Gleason ('26), recognizing gradation and that no two pieces of vegetation should be regarded as alike, proposed the individualistic concept. Sharp boundaries at abrupt changes in relief, soil material or land use are easily mapped but can be interpreted as irregularities in the continuum rather than as the foundation for a natural classification. Therefore, logical units will differ with different intended uses and often will be difficult to map.

The concept of vegetational continua has been reviewed by Goodall ('54). Whittaker (54), in summarizing a review of world literature on use of plants as indicators, stated: "Two fundamentally different indicator approaches are: the relation of classes of stands to classes of habitats, and the relation of gradients or functions of plant populations to gradients or factors of environment". The latter course has been most fruitful in interpreting range phenomena. Continua of both upland forest and prairie have been described by Curtis and McIntosh ('51) and Curtis ('55), respectively.

Many studies have helped to establish the degree to which relief and gradients in climate and soil are correlated with gradation in vegetation. Thus McBryde ('33), working in Texas, found over extensive areas, uniform in origin, resident soil factors and relief, that the effects of climate were reflected by gradual instead of abrupt changes in vegetation. Moreover, such changes along a climatic gradient were first shown by difference in amount or height of the vegetation, and then by difference in composition of the vegetation.

Jacks ('34), in a review of world-wide relations between soil, vegetation and climate, concluded that climate is the obvious basis on which to construct a world classification of genetic soil types, even though within small areas the association between soil type and type of vegetation is often far more pronounced than that between soil and climate.

Borchert ('50), a geographer doing research on the climate of central North American grassland, reported: "The vegetation gradients appear to coincide with the climatic gradients". On a continental plain he found the dominant factor controlling tempera-

ture and associated aspects of climate to be latitude, upon which a gradient in precipitation could be superimposed to account for the pattern of the grassland.

A unified system for subdivision and description of continua of climate and soil has been in use since 1949 in the five States of the Northern Great Plains, including deserts of Wyoming and the mountains of both Wyoming and Montana. The subdivisions and descriptions have been revised as needs arose in the continued application to new areas by range conservationists of the Soil Conservation Service, the Indian Service in South Dakota, certain field survey parties of the Bureau of Land Management in Wyoming and Montana, and through collaboration with all of the State college and university range faculty members within these States. A range site name consists of one of 20 soil-group names combined with a designation of the climatic belt and an abbreviation of the State name. The gradients of climate are subdivided by recognizing five belts with average annual precipitation from 5-9", 10-14", 15-19", 20-24" and 25-29", and limits of latitude and longitude for each, in this case specified by boundaries of five States.

The 20 soil-groups are arranged in the order of presumed potential foliage (not forage) production per unit of area with stable cover when undisturbed. The order, therefore, represents a gradient in the inherent productivity of the substratum for each climatic belt. The soil-groups are named as follows: Wet Land, Subirrigated, Overflow, Saline Lowland, Savannah Site, Sands, Choppy Sandhills, Sandy, Silty, Clayey, Dense Clay, Shallow, Panspots, Thin Loess, Thin Breaks, Gravel, Very Shallow, Saline Upland, Shale, and Badlands. The descriptions of each group will not be given here but are available. Thus range site names indicating soil and climate within limits of latitude and longitude designate units of the potential ecosystem for range management, based on non-living features. In using this procedure some 50 kinds of range land are recognized in Nebraska, and over 80 in Wyoming, on each of which range vegetation may vary from potential natural cover to wholly unnatural cover, or may be none as under bare fallow for wheat.

AGGREGATION AND COMMUNITY

The next principle to be recognized is that varying degrees of clumping are characteristic of the internal structure of populations. Such clumping among plants is caused by aggregation of individuals in response to local habitat differences and by reproduction and dispersal processes.

Populations from one or more species having mutual relationships among themselves and to their environment may be termed a "community" (Oosting, '56). The consensus that communities of plants are more reliable indicators of environment than individual plants was reached only recently (Sampson, '39). How communities or stands of range vegetation may be characterized in relation to site, utilizing principles of plant sociology, has been demonstrated by Hanson ('57). Community types may be differentiated in classifications of various kinds for various purposes. Community types are abstractions based on logic with objective though necessarily arbitrary criteria to meet specific needs.

Among all the kinds of organisms in a community, certain species or groups may stand out as dominant because of numbers, size or activities, while others are dependent upon them or merely subordinate. On ranges the dominant life forms are grasses, forbs and shrubs. They, therefore, receive most consideration in classifying range communities by types. Cain ('47) wrote: "Analyses of habitats and the description of environmental complexes . . . cannot take first place in the recognition and definition of plant communities. The plant life itself must be first," . . . but with recognition that community types are metaphysical approximations. Despite necessary approximations, the natural and stable types provide the logical basis for any classification of range sites.

In a study where soil separations were mapped within different categories of relief, Anderson and Fly ('55) reported that "Numerous subdivisions can be delineated on the basis of soil differences by those trained in soil classification methods. In this study statistical analyses of the populations of major forage species . . . have indicated that certain soils are sufficiently alike to support like plant populations and, therefore, sufficiently alike to be classed as a single range site". Their research led them to reduce 13 mapped soil units to six range sites.

Hanson and Whitman ('38), working in North Dakota, found

that over an extensive area with nearly uniform climate, there was definite relationship between soil heterogeneity and vegetation heterogeneity. They also found linkage between topographical position and the nature of the vegetation cover, pointing out that such linkage is best explained on the basis that different topographical positions present different environments for the development of both vegetation and soil. The author (Dyksterhuis, '46) arrived at a similar conclusion on a Texas prairie. That is, stratigraphy, through its effects on relief, had modified effects of climate upon development of both soil and vegetation. Therefore, local differences in ungrazed vegetation could often be correlated with either relief or soil. Recent synecological studies from Alaska (Hanson, '51, '53) to the Sonoran desert (Yang and Lowe, '56) have documented correlation of stable types of plant cover with soil characteristics.

Communities, as distinguished from community types, are sharply defined where there are abrupt changes in physical environmental factors or disturbances, but also sometimes without evident cause. In the Rocky Mountains a grass cover may meet spruce at a border like a wall without apparent cause and without apparent encroachment of one community on the other. Moreover, Braun ('56) believed that neither environmental gradients nor edaphic factors were adequate to account fully for distribution of the climax communities of the Mixed Mesophytic Forest region of eastern United States. McMillan ('56) has reviewed and demonstrated genotypic variation within phenotypes common to several communities in different environments.

Biomes (Clements and Shelford, '39), the largest most heterogeneous communities recognized, are most evident because their modal conditions are separated by the largest differences in origin and environment. However, boundaries of biomes are no less difficult to define than boundaries of lesser communities. Range and range evaluation must find at least its outside limits at the boundaries of certain biomes. This is not easy in a boundary between forest and grassland biomes where gradation through miles of savannah is to be expected, unless abrupt changes in soils offset climatic gradients (Dyksterhuis, '57).

Woodbury ('54) has enumerated four accepted bases for dividing communities. Briefly, on land, they are: (a) the conspicuous

dominant plants, (b) consistent membership in the community of specific organisms, (c) the type of climax biota the community will support, whether the climax is actually present or not, and (d) the environment in which the organisms live. All four are used in this system for determining the nature and number of range sites to be recognized.

STRATIFICATION AND PERIODICITY

Recognition of the principles of community stratification and periodicity is essential in range evaluation. It will help to avoid placing undue reliance on measurements or observations made just once. It will indicate limits of justifiable refinement in surveys of range vegetation. And it will enable observers to add mentally to or subtract from the population components of the vegetation at the time of observation, those amounts necessary to more nearly visualize the average condition of plant cover.

Vertical stratification is a characteristic structural feature of climax communities. Vertical differences in physical factors, such as temperature, light and oxygen, and in underlying soil or substrate are often directly responsible for stratification. Because of their almost complete interdependence, community strata are best considered subdivisions of the community rather than as separate communities. Stratification reduces interspecific competition and increases use of the solar energy impinging upon the area. On ranges, certain strata may appear only seasonally or only in certain years.

Periodicity is shown in more or less rhythmic changes in activities or movements of organisms and in the resulting regularly recurring changes in the complexion of the community as a whole. Among range plants, periodicity results mainly from seasonal rhythms in physical factors which directly or indirectly bring about periodicities in many component populations. Year to year changes in communities, due to differences in weather, are real; but alternations of annual weather between wet and dry, or warm and cool, appear too irregular from our present knowledge of them to be regarded as rhythms.

ECOLOGICAL SUCCESSION AND CLIMAX

Developmental communities can be interpreted according to the principle of succession which holds that there are orderly

processes of community change with a sequence of communities which replace one another in a given area until a relatively stable community in equilibrium with local conditions is reached. Such ecological succession is directional toward a point, stage or type, termed "climax". With study, successional changes and the climax for a developmental community can be predicted. Interplay of populations continues in the climax, but these fluctuations tend to be around an average instead of being a moving average.

In the applications of ecology to problems of deteriorated natural pastures we have come to rely increasingly upon what Clements ('35) termed ". . . the irresistible impulse toward the climax"; and a major corollary, ". . . that the climatic life-form everywhere maintains its ascendancy in the absence of disturbing processes". Moreover, there is increasing awareness that degeneration of climax vegetation resulting from overgrazing affects not only vascular plants but also the soil, where changes in content of water, air, organic and inorganic nutrients, and of microflora have been recognized (Daubenmire and Colwell, '42).

Different climates are associated with different climaxes. The climax of a climate is believed to be best viewed as a regional pattern of vegetation in which a prevailing and relatively stable type may be recognized on uplands of gentle relief with soils of medium depth and texture; normally with continuous gradation of vegetation along continuous and gradual environmental gradients, but also with zonation and discontinuity, especially in extreme environments and where environmental gradients are steep (Whittaker, '53, '54, '56). Examples of discontinuities are seen in local areas of forest climax within grassland climates, or grassland climax in forest climates, and in alternates of vegetation on alternating areas. The prevailing climax in a region is perhaps better regarded as a regional climax than a climatic climax because it is not a product of climate alone but also of past history measured in geological time (Braun, '56).

Primary and secondary successions are recognized. Primary succession occurs when new land surfaces or new bodies of water are first occupied by plants. On land, primary development of vegetation proceeds in equilibrium with development of soil as governed by climate. Primary successions, cliseres and geological

successions are of interest but too slow to be of practical concern in range evaluation.

Secondary succession is any succession after the primary following a disturbance that has not profoundly altered the character of the site. Clements ('35) wrote: "Every agency that destroys the vegetative cover and exposes the surface gives opportunity for erosion and flooding in proportion to the completeness with which it acts". Through succession the soil again becomes increasingly protected. "Such a protective function is peculiarly the property of the subseres, since this is initiated by disturbance on a soil readily susceptible to wear". A subseres, or secondary succession, can quickly restore equilibrium of plant community and soil, after which further development is the slow primary development of both soil and vegetation.

In range evaluation, knowledge of the site, its climax, and secondary succession, makes it possible to visualize vegetation beyond current plant communities and to predict changes in the vegetation that will tend to restore equilibrium in the ecosystem. Units of the non-living part of the ecosystem recognized in range evaluation are based on climax vegetation for several reasons. The physical environment, with all of its climatic and edaphic factors and their innumerable interactions and gradients, supports many measurably different plant communities in apparent stability with local site conditions. When grazing by domestic livestock is superimposed by thousands of owners with tens of thousands of pastures grazed in various ways, the climax pattern tends to be obscured, and there is an overall increase in the number of plant communities. Thus there are more kinds of range than of range land.

Secondary succession, if permitted by rest from grazing or by grazing practices that favor climax dominants, obliterates fence-line contrasts and reduces the number of communities while restoring the normal gradation of vegetation with gradients in the physical environment. There is a direct relation between secondary succession and conservation of soil and water (Warner and Aikman, '43).

RUDIMENTS OF APPLICATION

The type of climax vegetation that the environment will support is ascertained by interpolation and extrapolation from relicts.

Relicts of climax vegetation usually are small enough to involve but one macroclimate, and it is recorded. However, one relict area often shows two or more climax communities through zonation or a discontinuity in environment. Relative coverage, or annual foliage production, by species is recorded for each such community. Then soil characteristics of each are recorded, particularly texture and depth, plus any unusual amount of rock, salinity or wetness. From accumulation of such information a range site classification was developed and is frequently revised.

From comparisons of vegetation on native ranges with vegetation in relicts of climax, we have recorded which species decrease, increase or invade under grazing, *in each type of site*. We now have named environmental units of practical size for range evaluation and management, and know important differences in their climax vegetation. The environmental units, or sites, are related to differences in soil and climate ordinarily shown on soil-survey and climatic maps.

Range vegetation on the unit or site at the time of examination is expressed as one of four range condition classes, objectively based on a quantitative procedure described elsewhere, but, as Whittaker ('54) has pointed out, "The numerical determinations represent, essentially, relative positions along the gradients of retrogression or community disturbance for a given site, relative departure from the climax being defined by percentage similarity as an approach to 'ecological distance' along a gradient".

A recommended rate of stocking was assigned to each combination of range site and condition class by interpolating and extrapolating results on experimental ranges and from experience. Use of these rates by many stockmen in five states over the past six years has permitted secondary succession where needed for conservation of soil or precipitation, and has maintained the climax type on ranges classified in excellent condition.

A procedure for periodic remeasurement of surficial conditions and populations of range plants has been developed by Parker ('54) and is widely applied to determine trends in range conditions and rates of change.

SUMMARY AND CONCLUSION

Monographs by F. E. Clements, on plant succession ('16) the relict method ('34) and nature of the climax ('36) should be

credited for initial efforts to evolve this system of range evaluation based on ecological principles. Synecological studies on range lands, begun in 1939, quantified departures of current types of range vegetation from potential climaxes for specific sites (Dyksterhuis, '46, '48). Utilizing these and many other cited researches, along with widespread experience of the Soil Conservation Service, the synthesis of a new system of range evaluation, based on quantitative ecology, was reported ten years later (Dyksterhuis, '49). Since then there have been amplifications and some modifications among acceptable postulates (Dyksterhuis, '51, '52, '55) resulting from experience of many rangemen and from advances in ecology, especially those dealing with theory by Cain, Curtis, Odum and Whittaker. Rangemen and ecologists should find continued development and refinement of this range evaluation procedure possible if it is founded soundly upon ecological principles. This appears probable after a decade of testing under greater and greater diversity in conditions.

Yet, there are several limitations in practical application. Acceptable refinements in applied range ecology are dependent upon refinements in range management that are economical and acceptable by stockmen. Modern soil survey information is lacking in many range areas and not all rangemen are able to identify and map soil-groups such as those previously named. Data to properly establish gradients of precipitation and temperature are lacking in many mountainous areas. Many, if not most, ecologic descriptions of vegetation in the literature stress climatic and biotic but not edaphic features and avoid even "metaphysical approximations" of climax communities for various types of sites. Relicts of climax vegetation have not yet been found or reestablished in certain types of sites, making it necessary to assume a climax vegetation for them from established gradation along environmental gradients. Finally, application of ecological principles in range evaluation is limited by the ecological knowledge that professional rangemen have, and that graduates from range curricula are required to have.

There unquestionably is increasing acceptance and use of ecological precepts among rangemen. This is believed associated in large measure with an increasing number of active ecologists who: (a) seek earnestly to be understood by non-ecologists, (b) ac-

knowledge that acceptable examples of climax vegetation may be found or re-established in the absence of large influent animals such as the bison, (c) recognize that biological data may be useful even though inexact or not subject to exact mathematical expression, (d) discern but endeavor to reconcile polyclimax and monocl原因 viewpoints, (e) make it clear that grassland is not a stage in succession to forest when in grassland climate on grassland soil, and (f) accept fire as a part of the environment under which natural grazing lands were evolved and as closely related to climate, hence to a degree a part of climax conditions, particularly of climax grasslands rather than an unrelated phenomenon.

There is increasing awareness: (a) that evaluation of range communities must encompass not only organisms but also the physical factors of the environment, with the whole viewed as representing either dynamic equilibrium or imbalance between living and non-living features (i.e., of ecosystems); (b) that there is parallelism between gradation of climax vegetation, and gradients in climate and soil (i.e., of continua); (c) that differences in environment not reflected in different phenotypes may be reflected in different genotypes (i.e., of genetics); (d) that currently climax vegetation is a product of genetic, geologic and climatic history as well as of current environment (i.e., of interpretive plant geography); (e) that environmental factors produce organic responses while acting collectively, changing through the seasons and years, with action of each factor modified by other factors (i.e., of holocoenotic environment); and (f) that discoveries of parallelism between elements of physical environment and natural vegetation, though not interpretable simply as cause and effect, provide exceedingly useful data for many purposes including (i) evaluation of different kinds of range land when based on differences in kind or amount of climax vegetation and (ii) evaluation of different kinds of range cover that may occupy each of these kinds of land in range subseries.

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THE EFFECTS OF FLUCTUATIONS IN WEATHER UPON THE GRASSLANDS OF THE GREAT PLAINS

ROBERT T. COUPLAND

*University of Saskatchewan,
Saskatoon, Canada*

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