Land Management Policy and Development of Ecological Concepts¹

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Highlight

As ecological concepts become incorporated into the training and background information of professional land managers, they also become incorporated into land management policies. Recent developments in ecology, such as nutrient cycling studies and computer simulation of complex processes, have a favorable climate for acceptance. Possible applications should be carefully studied by land managers.

It is certainly paradoxical that in a world filled with hunger, the United States is constantly faced with the need to hold back on agricultural production. It is also disturbing to many of us who have worked for years to increase livestock production on rangelands that our efforts in this direction, although desirable from an individual viewpoint, are no longer critical from the national viewpoint. It is particularly frustrating because we have the technology to double or perhaps triple the production from our rangelands. Because of these facts, range managers have, in many cases, lost their sense of mission.

There are, however, more and perhaps greater things which need doing. I like to classify the jobs

²The author is Director of the Pawnee Site project in the Grassland Biome program of the U.S. International Biological Program. facing range managers today into the categories of (1) scientific understanding of the resource, (2) technological efficiencies (as opposed to technological possibilities), and (3) rural social adjustments. This order is not intended to assign any priorities to these three tasks; all are deserving of full consideration. This paper, however, will deal only with scientific understanding of the resource.

Theories are basic tools of science: all scientists need theories on which and with which to operate. It matters little whether the theory is correct, it must, however, be useful. Consider, for example, earlier theories of electron flow. Much electronic equipment was first designed with the belief that electrons flow in a certain direction around a circuit. As it turns out, electrons actually flow in exactly the opposite direction; nevertheless, circuits based on the original theory do work. Many other examples of operable, but inaccurate, theories exist. A theory, therefore, is to be judged not on the basis of truth, but on the basis of its usefulness. As long as the theory is useful, it very likely will not be replaced, but when the theory is no longer useful, it will eventually be replaced. The emphasis in this paper, for example, is intended to be provocation rather than accuracy, and hopefully the paper will have a short life.

Ecological Concepts of Existing Policies

Some early theories of ecology were developed from observations on the peat bogs of Europe, where several observers felt that the bogs developed through well defined stages. This reasoning was perhaps most notably followed in the United States by Clements (1916), who with Weaver (Weaver and Clements, 1938) developed a strong school of successional ecology based largely on observations in the sandhills of Nebraska. Clementsian ecology became the focal point of U.S. ecology for many years, and certainly received much impetus from the very practical management needs that were pointed out during the "dust bowl" days of the 1930's. Clementsian ecology, and other viewpoints of successional ecology, propounds that we first begin with bare rock which is converted by stages. These stages may include lichens and mosses, annual plants, perennial forbs, grasses, and finally, in appropriate climates, shrubs or trees. Such a progression is known as a xerosere. On the other hand, hydroseres, beginning with water but ending with the same climax condition, also can occur. If the progression from rock or water to the climax community is set back by any disturbance, and progression is then allowed to resume, the resumption of succession is known as secondary succession.

Most land managers in the United States today who are in a position to make policy decisions were most likely trained in successional ecology. In fact, concepts of successional ecology have been written into policy statements of many land management and advisory agencies. In some agencies, Clementsian ecology has become so entrenched in service policy that any one speaking out against these concepts, or even offering additional concepts, is considered a heretic.

Theories of successional ecology certainly have been useful. It was, for example, a most useful and necessary tool to recover from some of the earlier abuses in range management in the western United States. Certainly in many areas we have a long way to go before we can completely exhaust the benefits from successional ecology and its concepts. We have, however, continued to use successional ecology

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over and over until it has lost much of its usefulness. Much of the western range is in a condition where great progress from secondary succession alone cannot be expected. Most ranges are in much better condition than they were earlier, and we certainly have the necessary basic technology, if not the economic efficiency and political ability, to finish this particular job. In addition, Clementsian "sand hill" ecology has been pressed into use in areas where it was not conceived and where it is not quite so appropriate. Perhaps a few examples would be in order. In timbered lands, for instance, the progression towards climax does not necessarily equal a progression towards better conditions for range livestock. In fact, a climax coniferous forest is usually in very poor "range condition." On the other hand, a well established and well managed seeded range, by definition, is in a disclimax state because all of the species present are invaders, but, from the productivity standpoint, it may be excellent.

Although theories of successional ecology are still used by land management agencies, many range researchers have long since abandoned this concept as a fruitful area of research. They have, instead, turned to such fields as plant physiology, animal nutrition, and agronomy (including reseeding and brush control). This shift to similar, but more restricted, fields has, in part, been promoted by educational institutions which have been unable to offer solid training in range science as a total system concept. This search for meaningful research fields has led, in many cases, to fragmented research programs without a central theme, and has occasionally produced dichotomies between researchers and land managers.

Recent Trends in Ecology

Useful as successional ecology has been, it has become somewhat shop worn and is now being replaced on the theoretical front by a wide array of concepts and mathematical techniques and approaches collectively known as systems ecology. Since the term is used to describe a potpourri of the interesting and uninteresting, valid and invalid, and meaningful and meaningless, it would be impossible to cover systems ecology in a brief presentation. It is, however, possible to outline what seems a dominant concept as indicated by current interest of the scientific community, the probability of significant contributions of basic knowledge, and the validity of the use of the term systems ecology.

Tansley (1935) introduced the term "ecosystem" into the English language literature. Tansley's introduction of the term, however, was mostly a definition and it remained for Lindeman (1942) to clearly outline trophic (i.e., feeding level) ecology which has, in recent years, become a central theme for much ecological research. Lindeman happened to be an aquatic ecologist, and his paper on the trophic-dynamic aspects of ecology uses examples from aquatic communities. Nevertheless, the principles he outlined apply generally to other ecological systems.

Lindeman said that an ecosystem is a system made up of various compartments; the compartments are called trophic (feeding) levels and ordinarily include producers (or, more commonly, green plants), consumers (which in turn can be subdivided into primary consumers which eat plants, secondary consumers which eat primary consumers, etc.), and decomposers (which convert dead plant and animal matter back into carbon dioxide). Energy is received from the sun, and energy and matter are transferred among the various compartments. If we truly understood this transfer of energy and matter, we would then truly understand the operation of the system. If we understood these transfers so well that we could express them mathematically, we could then examine the effects of many manipulations of the ecosystem and predict many results without actually doing field experiments.

If we think about the few simple compartments outlined above (producers, consumers, and decomposers), we see that we could readily subdivide these compartments into growth forms, species, individuals, or parts of individuals. We could also consider many kinds of matter. Thus our concept of the ecosystem could very readily become entirely too complex to handle by ordinary bookkeeping systems. In addition, the measurements of transfers from one compartment to the other are in many cases quite difficult, and in Lindeman's time may have been impossible. In fact, many of them are still impossible, but introduction of radioisotopes as tracers and many sophisticated instruments have greatly facilitated and promoted studies of transfer processes.

For these very pragmatic reasons, therefore, trophic-dynamic ecology did not immediately arise to the forefront after Lindeman's original exposition. In fact, most of those attending universities over 20 years ago probably did not hear of trophic-dynamic ecology.

Modelling and Ecosystems

As noted above, when we subdivide the ecosystem compartments into the necessary functional complexity, the job of keeping track of the energy and matter flow among the various compartments soon becomes a major mathematical problem. Even for situations where the basic mathematical techniques are available very large problems could not adequately be handled until computers came into common use. At first computers were slow, large, and expensive to operate. As computers have become larger in capacity, they have also become generally smaller in size, faster in operation and, most important, much cheaper per job. Use of more complex techniques has become more and more feasible. More mathematicians, engineers, and now even biologists are becoming familiar with computer techniques. The development of mathematical tools used in analysis of feedback control systems is especially useful, and it it from this field particularly that much of the terminology of systems ecology is being drawn. An "adaptive control system with stochastic inputs" (Rosen, 1967), for example, sounds exactly like an ecological situation. The concept of an adaptive system, in fact, provides for union of the theories of successional ecology with the theories of trophic ecology if we consider an ecological system which is undergoing succession as a self-organized system (Margalef, 1968).

We now find arising today a considerable number of mathematically-oriented biologists, and biologically-oriented mathematicians and engineers, who are attacking the problem of trophic-dynamic ecology. It is something of a basic ground swell among ecologists. In fact, we can say with certainty that complex ecological systems will be investigated from the standpoint of trophic-dynamic ecology and systems engineering. The only question, since science does progress as a body, is who is going to do it best.

It happens that at the moment the primary worldwide research effort in this area is centered about the International Biological Program (IBP). Particularly in the U. S. these efforts are imbedded in the integrated IBP research program on the Analysis of Ecosystems (AOE). A number of IBP Biome programs have been organized within the AOE including the Grassland, Desert, Eastern Deciduous Forest, Western Coniferous Tundra, Forest, and Tropical Biomes. Of these biome programs, the Grassland was selected for the first major effort because of (i) its seeming simplicity, (ii) the location of a suitable intensive study area, namely the combined areas of the Pawnee National Grassland and the Central Plains Experimental Range, known in IBP circles as the Pawnee Site, (iii) the rapid and extensive cooperation of a suitable

	from to (time t) (time t+2	↓ (Live plants	Standing dead	Plant litter	M i crofiora	Soil Organic Matter	Herbivores	Omnivores	Carnivores	Soil fauna	Animal litter
		C ¹	C ₂	Сз	C4	С ₅	с ^е	с ₇	C ₈	С ₉	CIO
cı	Live plants	-1	+	+	+	+	+	+	ο	+	о
C2	Standing dead	0	-1	+	+	+	÷	+	0	0	о
C3	Plant litter	0	0	-1	+	+	0	0	0	+	0
C ₄	Microflora	0	0	0	-1	+	0	0	0	+	0
с ₅	Soil Organic Matter	+	0	0	+	-1	0	0	0	+	о
C ₆	Herbivores	0	0	0	0	+	-1	+	+	0	+
C,	Omnivores	о	0	о	ο	+	ο	-1	+	0	+
с ₈	Carnivores	0	0	0	0	+	0	+	-1	0	+
c,	Soil fauna	0	0	0	+	+	0	+	+	-1	+
c _{io}	Animal litter	0	0	0	+	+	0	0	0	+	-1

FIG. 1. A matrix of transfers between compartments of a closed system. Here, 0 = no transfers, -1 = diagonal elements, and + = transfer between compartments. The sum of all positive numbers in the columns of this figure will be +1, so that for closed systems at steady state the total transfer to each compartment will sum to zero.

pool of scientific manpower available at the several major nearby universities and colleges and associated federal research organizations, and (iv) the obvious dependence of man on the grasslands of the world.

Matrix Representation of Ecosystems

We have stated above that an ecosystem is a system which transfers energy and matter from one compartment to another (for a further discussion see Margalef, 1968). If we have "n" such compartments, we can describe a greatly simplified ecosystem as a "n \times n," who-eatswhom matrix in which the elements of the matrix describe the rate of transfer of energy or matter from each compartment at time "t" to each of the compartments at time "t + Δt " (Fig. 1). If we knew the individual coefficients or mathematical functions for all such transfers in this matrix, we could then claim to understand the function of the ecosystem. In Fig. 1, I have entered some zero coefficients, but scientists involved in the study of various transfers will make the case that, in the strictest sense, there are very few zero transfers. At this point, however, the matrix is most important to point out an approach.

Ingestion of herbage by herbivores is one transfer process-in this case the transfer between live plants and a particular herbivore species. The rate of this transfer process becomes an element in our who-eats-whom matrix. Biologists have been working on the determination of many of these transfers for some time, but others have not received a great deal of attention. In fact most of the energy and matter transfers cannot be measured directly. Therefore if we are to say that we understand an ecosystem by knowing where energy and matter flows in the system, we must find some other procedure.

An Analytical Approach

An alternative is to determine the amount of energy and matter in each compartment at several

points in time. With these data points in hand, we can arrive at a solution of the " $n \times n$ " matrix of coefficients which describes the flow of the matrix using solution techniques as outlined by Berman et al. (1962a and 1962b) and Bledsoe and Van Dyne (1968).

To facilitate solution we can utilize any knowledge we have concerning transfers, that is, we can provide constraints for the elements of the matrix. For the most part we may guess the zero or near zero coefficients from past experience. These analyses give us our first approximation which is a linear, constant-coefficient model. Additional information is required to develop more realistic nonlinear models, which we have every reason to expect will be required to describe real world events. The same basic analytical procedure, however, can approximate nonlinearities and discontinuities through linear segments (Bellman and Roth, 1966).

With such a model in hand, various forms of sensitivity analyses can be made. One can investigate stage by stage the effect of modifying the system; i.e., one can change a coefficient of the model to determine the overall effect on the compartments many stages later.

Spatial Relationships

The matrix presented in Fig. 1 represents changes in time. In trophic-dynamic ecology, point space is usually assumed. If we expanded the matrix in a third dimension representing spatial distributions we would then have a representation which would cover various areas. People other than mathematicians ordinarily consider a space as being distributed; that is, from any point to any other point it is possible to be at any intermediate location. The mathematics of such a system, however, become quite complex. It would be much easier mathematically to consider space as lumped so that pastures, soil mapping units, etc., become discrete units.

Open Systems

We can consider two forms of constant coefficient models-a "closed" form and an "open" form. These mathematical properties also have important relationships to biological problems. A system can be considered "closed" if we can actually measure all compartments. If we are unable to measure the amount of matter or energy in any of the compartments, the system is "open" and we will not be able to obtain a direct solution from the method presented above; therefore we must have a measure of all transfers to and from compartments which we cannot measure directly. In other words, we must measure all input to and output from our otherwise closed system.

On many semi-arid rangelands we have reason to believe that because of low fixation and low loss rates it may be possible to approach the study of nitrogen transfer by a closed system approach with only minor errors. We know, however, that carbon cycling and energy transfers must be considered an open system. A knowledge of the carbon dioxide fixation rate through photosynthesis studies then becomes an important part of a total systems study. In addition, losses of carbon and energy from the food chain require studies of plant and animal metabolism, and losses of soil moisture require studies of evapotranspiration to elucidate losses from the various compartments to the outside atmosphere.

Forcing Functions

In ecology, the text by Daubenmire (1947) represents the study of the effects of environmental forces on components of the ecosystem. In the language of systems engineering, such outside forces which cause changes in the system are called forcing functions. The time required for the system to return to "normal" after it has been influenced by some outside force is called transient time and the "normal" situation is called the steady state. By analyses of the output of a system when forced or perturbated with a known input, we are able to determine the transfer function of the system, which is the ratio of the output to the input. Once we determine the transfer functions of the system, we can build a system simulator and replace these standardized inputs with the variable forcing functions which occur in nature, and observe the system behavior under these conditions. Such concepts have been widely and profitably used in some fields of biology (Milsum, 1966) but have not been commonly used in ecology.

In rangeland ecosystems highly probabilistic rainfall is the chief perturbation or cause of noise. A better behaved forcing function is solar energy. We have been hampered a great deal in the past by the fact that climatologists prefer to express their data in terms of some sort of averages. Weather, however, is not average, but probabilistically variable, i.e., stochastic, and in a study of the effect of forcing functions on the operation of the ecosystem we need to describe climate by the parameters which point out these probabilistic properties. There are various ways to represent climate by the characteristics which determine its variability so that it can be used in computer simulation (e.g., Pattison, 1965), but we will not go into these methods here.

In the past few paragraphs I have described an approach which represents mathematically the function of a range ecosystem. The core of this approach begins with the constant-coefficient closed system which is represented in the " $n \times n$ " matrix of constant transfers between "n" compartments. This basic system was first expanded to include spatial relationships, further expanded to allow inputs from outside the system primarily in the form of carbon dioxide fixation, and outputs from the system primarily in the form of carbon dioxide release and evapotranspiration. Such a system would become quite stable were it not for such influences as rainfall and solar energy, which shock the system out of its steady state.

System Behavior

How do such systems behave? For many range ecosystems manipulation of grazing animals causes a significant change in the nature of the producer compartment of the ecosystem. This impact of grazing on range plants has, of course, been the central theme of range management. If we had a study area, however, which has reached some equilibrium with grazing, the year to year changes can be considered to be random events. The annual values in a purely cyclic system show no change and are not particularly useful for systems analysis. There are, however, changes within years. This points out that in the study of an ecosystem which is relatively stable we can probably learn more by a study of seasonal rather than annual effects.

The seasonal changes in any population, regardless of how complex they may be, can be represented to any arbitrary accuracy by a series of sine and cosine terms. Such equations, although they can describe the behavior of a system, do not help show how it works. As we learn more about the system we are able to develop more mechanistic models; that is, we are able to predict more and more precisely the response to various inputs, add terms to the equations describing system behavior as a function of these inputs, and delete terms showing responses as a function of time.

Models and Simulators

We have progressed from a rather simple constant-coefficient, closed system model to a spatially disturbed, nonlinear, open system with random environmental effects and system responses which are functions of probabilistic inputs. This build up from simple to complex models has been a most useful approach in systems analysis and simulation in many fields. For example, Forrester (1961) observed: "In engineering systems models have been built upward from available knowledge about separate components. Designing a system model upward from identifiable and observable pieces is a sound procedure with a history of success.

In economics, models have often been constructed working backward from observed total systems results. Even as a theoretical goal, there is no evident reason to believe that the inverse process of going from total-system behavior to the characteristics of the parts is possible in the kinds of complicated, noisy systems that are encountered...."

Computer simulations of a great number of biological phenomena are becoming more and more common, and proper use of simulation techniques can be very effective in resource management planning. An example in range management is the work of Goodall (1969). Examples of several simulators in other fields are cited by Watt (1966, 1968).

Simulators and other models are useful in organizing and describing existing knowledge about a particular system, and point out areas where new studies are needed. They may include analytical techniques such as described in this paper or techniques borrowed from business and economics (e.g., Hein, 1967), generally are built from but many simple relationships, utilizing knowledge and concepts of individuals or teams of individuals who are thoroughly experienced in a particular area. In short, useful simulators are built not so much from complex techniques as they are from experience and hard work.

New Land Use Policies and Research Possibilities

In the beginning of this paper I stated that successional ecology has, in the past, been so useful in range management that it has, in fact, become embedded in the policy of land management agencies. Whether or not trophic-dynamic ecology can be utilized in resource management to the same degree remains to be seen. I have observed, however, that not only ranchers but city dwellers as well seem to be able to understand the basic concepts of trophic-dynamic ecology much more easily than those of successional ecology, and it appears from the public and congressional support of the IBP that trophic-dynamic ecology can be a program which is much easier to "sell" than successional ecology. Nevertheless, much of our background information is in terms of successional theories, and to make greatest use of this information we should seek integration of the various schools of thought.

Several years ago a prominent Southwestern rancher asked if there wasn't some way to include new ideas, such as energy flow studies, in range research programs. Certainly ranchers are extremely interested in how much energy and matter flows from the producer compartments to the large herbivore compartments, much more so that they are in the successional stage of a particular range, and we all are concerned about how our technological disturbances of some compartments of the ecosystem may influence other compartments of the ecosystem in which we live. In addition, properly formulated and operating models of trophic-dynamic and other systems allow us to explore many land management alternatives without actually applying treatments in the field. This could be an extremely valuable tool.

At the moment we are not prepared to incorporate large pieces of trophic-dynamic ecology into land management agencies' policies, particularly since the first attempts to be realistically complex in such investigations are just now beginning. I think it is appropriate for land managers, both public and private, to encourage research in new aspects of ecology and to begin to explore new ways which these modern concepts can be incorporated into land management guidelines.

As in any new field there will be many false starts and inefficiencies.

Obviously the skills required soon exceed the abilities of any one individual, and team research is required. An ideal institution for such complex research would have flexibility and access to a wide variety of individual specialties, and at the same time a critical mass of interdisciplinarians with dedication to, and time for, the necessary integration between the various specialties. Large universities (or several nearby universities) and their associated federal research organizations do have a wide variety of intellectual skills, although we are finding that in certain specialty areas people do not exist even in five universities. This complex effort, however, requires new concepts in integration, unity of purpose, continuity of personnel, and administrative efficiency which previously have not been universal attributes of universities. We find that necessary structure and teamwork can be developed once the individuals concerned become convinced of the urgency of the problems and the benefits of cooperative research.

The payoff from such research could be great, or, like any research, the direct payoff in terms of applied management practices could be nil. It appears very probable, however, that investigations into new concepts of ecology will more likely be profitable than many things which we have done in the past in rangeland research and will provide a basis for rational resource decisions in the future.

Literature Cited

- BELLMAN, R., AND R. S. ROTH. 1966. Segmental differential approximation and biological systems: An analysis of a metabolic process. J. Theoret. Biol. 11:168-176.
- BERMAN, M., M. F. WEISS, AND E. SHAHN. 1962a. The routine fitting of kinetic data to models. A mathematical formalism for digital computers. Biophys. J. 2:275–287.
- BERMAN, M., M. F. WEISS, AND E. SHAHN. 1962b. Some formal approaches to the analysis of kinetic data in terms of linear compartmental systems. Biophys. J. 2:289– 316.
- BLEDSOE, L. J., AND G. M. VAN DYNE. 1968. Evaluation of a digital computer method for analysis of compartmental models of ecological systems. Oak Ridge Nat. Lab. TM-2414.
- CLEMENTS, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Inst. Pub., Washington, 242:1-512.
- DAUBENMIRE, R. F. 1947. Plants and environment. John Wiley and Sons, Inc., New York. 424 p.
- FORRESTER, J. W. 1961. Industrial dynamics. The M.I.T. Press. 464 p. GOODALL, D. W. 1969. Simulating the grazing situation. In F. Hein-

mets [ed.] Concepts and models of biomathematics: Simulation techniques and methods. Marcel Dekker, Inc.

- HEIN, L. W. 1967. The quantitative approach to managerial decisions. Prentice-Hall. Englewood Cliffs, N.J. 386 p.
- LINDEMAN, R. L. 1942. The trophicdynamic aspect of ecology. Ecology 23:399-418.
- MARGALEF, R. 1968. Perspectives in ecological theory. The Univ. Chicago Press. 111 p.
- MILSUM, J. H. 1966. Biological control systems analysis. McGraw Hill. N.Y. 466 p.
- ODUM, E. P. 1959. Fundamentals of ecology. 2nd Ed. W. B. Saunders Co. 546 p.
- PATTISON, A. 1965. Synthesis of hourly rainfall data. Water Resources Res. 1:489-498.
- Rosen, R. 1967. Optimality principles in biology. Butterworths, London. 198 p.
- SMITH, R. L. 1966. Ecology and field biology. Harper and Row. N.Y. 686 p.
- TANSLEY, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.
- WATT, K. E. F. 1966. Systems analysis in ecology. Academic Press. N.Y. 276 p.
- WATT, K. E. F. 1968. Ecology and resource management. McGraw-Hill. N.Y. 450 p.
- WEAVER, J. E., AND F. E. CLEMENTS. 1938. Plant ecology. McGraw-Hill. N.Y. 601 p.

THESIS: UNIVERSITY OF WYOMING

Preference and Utilization Trends by Cattle on Grass-Forb Vegetation in the Northern Big Horn Mountains, Wyoming, by Lynn D. Todd. M.S. Range Management, 1969.

Vegetative preference and trend of utilization shown by cattle on the northern Big Horn Mountains of Wyoming was measured during the summer of 1968.

Two study areas were selected. The first was at an average elevation of approximately 8,600 feet while the second was at an average elevation of 9,300 feet.

The livestock preferred grasses and sedges over forbs. The major preferred grasses and grasslike plants were Agropyron spp., Koeleria cristata, Poa spp., Stipa spp., and Carex spp.

The major preferred forbs were *Taraxacum officinale*, *Agoseris glauca*, *Polygonum bistortoides*, and *Arnica* spp. There was some difference in preference shown for forbs between the two elevational sites.

Some degree of utilization trend was shown for most species. The most definite and most explainable trends were found to be in forbs. Utilization trend in grasses and sedges were not as explicit.