COMPARISON OF THREE RANGE ECOLOGICAL MODELS: WHICH AND WHERE FITS THE BEST A REVIEW

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Introduction

Rangeland condition assessment that is used to facilitate decision making in management of range resource has been under discussion for the last decade. Ecologists in various parts of the world have questioned the validity of earlier method of assessing range condition particularly the Clementsian model based on plant succession and climax (Friedel, 1991, Laurenroth & Laycock, 1989). New thoughts are provoked on the way of this discussion and new ideas and approaches are emerging. The necessity of new ecological models was realized keeping in view the limitations of the successional model in meetinig the management objectives of a particular range resource in a given set of ecological conditions. The paper reviews the major approaches of three ecological models and discusses their validity and application in varying sets of ecological conditions.

Materials and Methods

A vast body of literature on range ecology was reviewed and the concerns of various range scientists about the limitations of successional model were taken into consideration, At the same time, alternative models being presented by range ecologists for assessing range condition under various climatic regions of the world were discussed. The pros and cons of these models are presented to the range scientists and managers to help them arrive at valid conclusion for making wise decision to better manage and utilize the Rangeland resources under given set of environmental conditions,

Discussion

Successional Model

The Successional model was derived from the Clementsian ideas of plant ecology and based on these ideas Dyksterhuis in 1949 put forward the 'Quantitative Climax Method (QMC) which was adopted by US government agencies as a system for rangeland classification (Dyksterhuis 1949, Smith 1978, 1988, Westoby et al.1989). Later on, this idea got established into the

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range profession and range ecologists treated it as a 'holy word' spanning over almost a quarter century. According to this model succession is a linear change of vegetation in the absence of any disturbance. This leads to a pristine state or 'climax' which is considered as a bench mark for measuring rangeland condition and is termed as the desired state for any vegetation type (Tueller 1973, Smith 1979, 1988. Westoby et al. 1989). The reason this model gained so much popularity was based on its simplicity (and probably because of its connection with the Society for Range Management, established in 1945). Vegetation succession towards Climax State is thought to be a steady process. Succession, basically is divided into primary, secondary, autogenic and allogenic types. During primary succession, plants colonize bare sites such as sand dunes, volcanic mudflows and marshes etc. (Colinvaux 1986). Secondary succession follows the primary succession by relatively higher order plants. Secondary succession after disturbance is regarded as autogenic succession resulting in better site conditions to accommodate more demanding plant species to set in Smith (1988). The species establishing in result of autogenic succession may be more specialized and competitors. If no disturbance occurs, this process may continue towards a predicted endpoint commonly known as 'Climax'. Smith (1978) states that climax is not a static state, it rather oscillates around its mean because of variation in biotic and abiotic factors. As a result of disturbances such as fire, drought, grazing or other natural catastrophes, it may undergo different sets of species composition of relatively lower successional order. The important point in this concept is that once the disturbances are removed, the plant community will follow the same successional path that leads towards c1imax. The time span of retrogression may, however, vary depending upon factors like the extent and impact of disturbance, soil and climatic variables, seed source and the amount of colonizing plant species, etc. (Smith 1988).

Limitations of successional model

There are certain constraints associated with the use of Quantitative Climax Method of successional model (Smith 1978, 1988; Westoby et al.1989, Laycock 1991). These problems are discussed briefly as under:

1. This model can not identify climax species composition.
2. It is more specific to temperate perennial grasslands.
3. It does not accommodate desirable introduced (exotic) plant species. In strict sense of climax, exotic species are not part of the climax and thus these species are ignored while rating the rangeland condition.

4. It defines forage species as decreasers, increasers and invaders. This classification is more livestock oriented.
5. According to this model, retrogression and succession follow parallel and identical pathways. If disturbance is removed the range vegetation is supposed to return to the original Climax State.
6. It ignores site potential in a given landscape. Some agencies use some scores for rating site potential which include the variables like species composition, productivity, erosion etc. with less regard to other factors, e.g., slope, soil type, topography, aspect, soil moisture etc.
7. It assumes that change in vegetation is mainly because of livestock grazing although other factors also play their role.
8. This model gives the impression that things happen in a continuous way i.e., excellent to good to fair to poor while one state may jump to any of the lower states depending upon the force being applied on the system.
9. The classes (excellent, good, fair and poor) have very sharp boundaries.
10. The climax vegetation may not be the desirable state from a given management.
11. Public sector reports on range condition based on climax approach are often misleading because of different criteria (as poor, good, fair or excellent) used by different agencies.

Based on the limitations of the successional model, Smith (1978) concluded that this approach is inadequate and needs to be modified to meet the management objectives.

Equilibrial and Non-equilibrial Model

Quite recently, based on their experience in arid regions of different continents, ecologists have demonstrated that climatic changes in various rangelands drive the system away from the stability. The climatologists have analyzed severe climatic variations on large spatial and temporal scales. These variations imprint long-lasting effects on the natural flora of rangeland.

Keeping these variations in view, ecologists developed models to better understand the impact of climatic changes on plant populations on one hand and interactions of plants with the herbivores, on the other. Ellis (1993) describes that new models fall into two general categories: those, which emphasize that high climatic variability drives the plant-plant and plant-herbivore interactions (non-equilibrial or chaotic models) and those, which emphasize the state and transition model. In either case, the authors of these models question the validity of successional model in ecosystems where high instability occurs.

The non-equilibrial model considers the prevailing climatic variation and its impact on vegetation production and dynamics of herbivore populations. Unlike the successional model, this system considers that herbivores cannot be held sole responsible for inducing changes in plant populations, rather climatic variations are the major forces driving the vegetation dynamics.

DeAngelis and Waterhouse (1987) discuss that models have been developed, assuming that plant populations are in a state of equilibrium. The existence of such a state requires the assumption of density-dependent population growth. The practical difficulty with such a state is that it can not be extrapolated to a smaller spatial scale on which observations are mostly made. Authors quoted the example of logistic equation describing population number, N.

$$dT = r(1-N/K)N$$

Population number, N has a stable equilibrium point N = K, which fails to describe the dynamic state (deviation from equilibrium) on a smaller spatial scale. Since dynamics of population on smaller spatial scale is important in ecological systems, thus there is a need to modify logistic equation. DeAngelis and Waterhouse (1987) used a cup and ball analogy to describe that equilibrium and stability is not applicable in real systems (Figure 2).

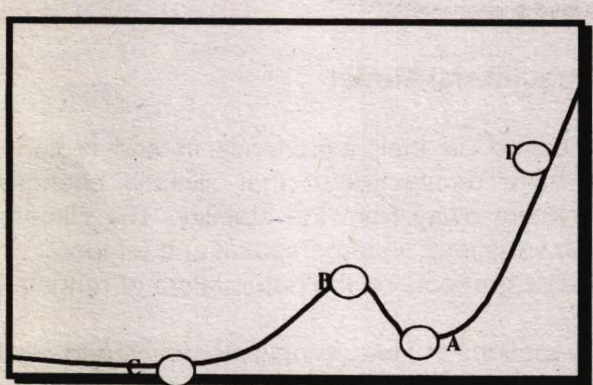

Figure I. Cup and Ball analogy describing equilibrium and stability (Source: DeAngelis and Waterhouse, 1987, p. 2)

The figure above shows four balls at four different positions, A, B, C and D. In each case the ball can be considered in an equilibrium situation, but the relative stability differs with respect to the position of the ball. Ball A seems to be relatively in more stable situation than other three balls but any force can displace it towards B and it cannot return to its original position. Similarly any force can kick the ball from position A to position D from where it can overshoot, never to return to position A. Ball at point B is in unstable position. It can roll either towards A or C. Ball at point C is neutrally stable and its displacement will have no tendency either to come back on its original position or move away from it. Authors suggest that description of cup and ball analogy provides a poor guide in understanding equilibrium and stability since the situation in the real world is more complex and stochastic. Weins (1984 a, b) quoted by DeAngelis and Waterhouse (1987) further divided the ecological communities as stable equilibrial systems (driven by biotic forces, few stochastic effects) and non-equilibrial systems controlled more by the environmental variations such as storms and droughts.

Ellis (1992) mentioned the example of drought stressed east Australian ecosystem where Kangaroos and sheep are the main herbivores. The rainfall is highly variable ranging from 200-300 mm annually (with a 45% coefficient of inter-annual variation). Floods and droughts are common features of this region. There is tremendous effect of drought on the plants and the herbivores. Species composition, dominance, forage yield and changes in life forms are more pronounced with respect to rainfall than grazing. The past 100 - year record confirms this pattern of plant and herbivore dynamics. Based on the past history and computer simulation models, it is argued that due to high climatic variance in the region, the concept of carrying capacity based on the successional model is of little value in this situation and understanding of the system.

In view of the foregoing discussion, one can argue that arid and semi arid ecosystems can be categorized as in non-equilibrium state where climatic factors are major forces defining ecosystem's direction on large spatio-temporal scale.

State and Transition Model

This model is based on the fact that a rangeland ecosystem is influenced by long-term climatic, edaphic (and sometimes pyric) factors. These factors or forces may drive the system to a stable state that could prove to be resistant to management operations. Once any factor forces the system to cross a threshold, it may not be possible for the management to drive the system back to its original state within a reasonable timeframe. Westoby et al. (1989) mentioned that discrete states, and transitions between these states could present rangeland dynamics. Laycock (1991) defines the states as "recognizable and relatively stable assemblage of species occupying a site and the transitions between the states are triggered either by natural events (e.g., weather, fire) or by management actions (e.g., grazing, destruction or introduction of plants). Westoby et. al., (1989) also mentioned that transitions between the states can be changed to the next one by factors like climate or fire and/or by management or a combined effect of all these forces. Transitions are considered to be changing and a system can not come to rest between the transitions. These states and transitions could be visualized by the following diagram presented and explained by Westoby et al. (l989).

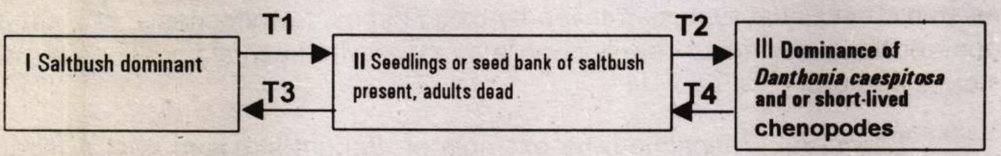

Figure 2. State and transition diagram of Bladder saltbush (*Atriplex vesicaria*) on heavy clay soil in the Australian Riverian Plain. (Sources: Westoby et. al. 1989).

In the diagram above, State I represents dominance of *Atriplex vesicaria* having more than 20% cover with lesser contribution of *Danthonia caespitosa* bunchgrass and number of short-lived chenopods. State II represents dominance of Danthonia bunchgrass and short-lived chenopodes with soil seed bank and seedling population of *A. vesicaria*. State III is similar to State 2 except absence of seed-bank of *A. vesicaria*. This state is satisfactory from the pastoral production point of view with no threat of soil erosion. Transition I represents100% defoliation of *A. vesicaria* due to increased grazing. In transition 2 seedlings of saltbush (*A. vesicaria*) germinated after rainfall but survival of these seedlings is less due to unfavorable weather conditions and also due to grazing by sheep. Transition 3 represents enough rainfall for seeds to germinate and seedlings to survive and reproduce. Grazing is also absent. Transition 4 is similar to transition 3 but an external source of saltbush is required (Westoby et al.1989).

Under the conditions explained above, the management has to be vigilant enough to respond quickly as to augment favorable thresholds and avoid unfavorable ones. Once a threshold is crossed, e.g., state I to state II, substantial resources are required to bring the system back to its original state. Noy-Meir and Walker (1989) define stability as "the ability of the system to remain the same while external conditions change". The authors argue that there is a problem of measuring stability and resilience in the field, but this difficulty can be overcome either by developing analytical models of the system based on appropriate data or by obtaining empirical measures from the analysis of the dynamic behavior of the system under natural or experimental conditions. May (1977) mentioned that there is no doubt that multiple stable states do exist in ecosystems, however, the state which a system possesses may depend on the initial conditions and a system may return to this state following small disturbances but large disturbances may carry it to a new state. Thus the system behaves like the ball in a pinball machine. Friedel (1991) proposes to focus on thresholds of change from one state to another. She argues that range does not deteriorate linearly rather it retains the capacity to recover up to a critical point. Beyond this critical point, the system may not return to its original state.

The state and transition model could be well visualized having in mind the situation prevailing in north-eastern grasslands of highland Balochistan province. Here, dominant plant community earlier consisted of *Cymbopogon jwarancusa* and *Chrysopogon aucheri* (Saleem and Call 1993a). The former species contains a chemical compound known as Piperitone that hinders its palatability. *Due to* Piperitone, *Chrysopogon* is selectively grazed by the livestock providing a chance for *Cymbopogon* to spread. In another transition, the increased grazing pressure has resulted in decrease of *cymbopogon* grass and invasion of relatively low palatable shrub *Artimisia maritima* (Saleem and Call 1993b). Thus in highland grassland, one could find vegetation in different transitionery states, while changing grassland into a shrubland. If these thresholds are not reversed by a wise management, highly productive grasslands will change into low productive shrublands making difficult for the management to reverse these processes in a reasonable time frame and within limited available resources.

Based on the view points of various authors discussed above, it is, however, evident that the state and transition model is relatively new theoretical approach and yet considerable research is needed to devise a methodology to identify different states in natural plant populations and the ways to keep the system in a desirable state. From the foregoing information it is also obvious that successional model is not considered adequate for the assessment of range vegetation condition trend due to its weaknesses discussed earlier. In spite of these weaknesses, we should, however, admit that this model has provided a platform to the ecologists to put forward the concepts of vegetational changes through different seral stages leading towards climax. Models, everywhere in each discipline, are not always perfect, rather resistance to changing ideas is very strong even in the face of research. These models could further be improved over time through a process of continuous research and practical application on ground. Regardless of its inadequacies, successional model seems to remain under use at least as a teaching tool in ecological fields to demonstrate the dynamics of vegetation on different spatio-temporal scales. This model will also remain under use in range management circles, in various parts of the world until such time that ecologists come up with more practical and easy to use models.

State and transition and non-equilibrium models do provide strong theoretical and conceptual background about various variables while assessing the range vegetation trend particularly in arid and semi-arid rangelands. These models, however, lack a definite methodology to work with and also both of these models share some complexity regarding their applicability under different sets of ecological conditions. Their validity at the moment is thus questionable since both rely primarily on the influence of abiotic factors on vegetation in contrast to successional model that heavily focuses on biotic factors. Another contrast between these and the successional model is that successional model is considered to be more valid for temperate climate which is considered to be relatively stable compared to arid and semi-arid tropical ecosystems where uncertain and unpredictable climatic variables play a havoc with the natural vegetation. Keeping these points in view, some critical questions asked by various ecologists are:

1. What kind of changes do we expect in ecosystems driven by climatic fluctuations and regarded under non-equilibrial state?
2. What are those forces which do not allow a system to re-occupy former state once they cross the threshold point?
3. Are these new models compatible or do they simply present different timeframe analysis?
4. What should be the strategy to manage extremely dynamic rangeland ecosystems?

We need answers to all of these questions

Conclusion

Although state and transition and equilibrial models do provide a comprehensive conceptual framework about the dynamics of vegetation in ecosystems primarily driven by abiotic factors such as climatic events and influenced by changes in soil and pyric regimes, they lack a clear methodology to be followed for assessing the range vegetation trend. Considerable research is required to devise a sound procedure to be adopted in different ecologies for assessing trends in vegetation through these models. Until such time, successional model can be used as a benchmark model with suitable modifications according to the prevailing climatic conditions in different parts of the world. Successional model then can be replaced whether by state and transition model or by equilibrial model (or any other suitable model developed in due course of time) once these models come up on a reliable consensus regarding their methodologies.

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