# State and transition models for rangelands. 2. Ecology as a basis for rangeland management: Performance criteria for testing models

JOEL R. BROWN

Division of Tropical Crops and Pastures,

CSIRO, Townsville, Queensland, Australia

## Abstract

The objectives of this paper are to: propose criteria for testing the applicability of models for rangeland management; and test 2 competing models using those criteria. Predicting change accurately, detecting change, relevance to management and facilitating communication are the performance criteria. Competing models are the range condition model derived from Clementsian ecology and the state and transition model based on non-equilibrium ecology. The ability of competing models to predict ecosystem change is assessed in terms of ecosystem organising processes and attributes such as competition, resistance and resilience, temporal thresholds and feedback. The ability to detect change is viewed in terms of detection at the community and landscape scales. Relevance to management and communication are assessed within the context of effectively communicating the effects of management decisions on ecosystem processes to both traditional and non-traditional decision makers and a larger public constituency. Although the state and transition model is the most acceptable of the 2 competing models based on the criteria, improvements are needed. Most notable is the need for a spatial component in the application of the model for management purposes, and the need for attention to improved communication with a wide range of resource users.

Correspondence: Dr J.R. Brown, CSIRO Division of Tropical Crops and Pastures, PMB, PO Aitkenvale, Qld 4814, Australia

### Introduction

Range management, the economic exploitation of rangeland ecosystems, should be inextricably linked to ecology, the science of the interaction of organisms and their environment. Although disciplines other than ecology may offer scope for improving management, success has been limited at best. Attempts to apply principles and techniques from more intensive agriculture (agronomy, weed science) have had limited positive impact in areas such as reseeding abandoned cropland or restoring degraded land. Animal science has provided very little in terms of more sustainably managing rangeland ecosystems (Gardener et al. 1990). In fact, improvements in animal-based technologies have generally resulted in increased exploitation, and decreased sustainability, of rangeland ecosystems (McCown and Williams 1990).

The economic realities of managing rangelands dictate that cultural inputs be minimised and used as effectively as possible. Low profit margins per unit area limit potential return on investment over any reasonable planning horizon. The temporal variability of most rangelands also requires that economic risk be minimised for any given time period. The mixed vegetation lifeforms, highly variable environments and selective grazing habits of wild and domestic herbivores impart an instability that requires managers to subtly direct ecological processes and limit highcost inputs to achieve objectives. As a rule, the success of "range improvement" practices reflects more the ability of a manager to direct ecological processes aided by technology than the effectiveness of the technology itself (Scifres 1987).

Applied ecology, therefore, remains the most likely basis for successful rangeland management. Process-oriented conceptual, graphical, and mathematical models that accurately represent

the current state of ecological understanding are needed to develop, communicate and implement effective management strategies. To extend knowledge beyond specific situations and unify understanding, attention should focus on how management interacts with ecological processes and affects ecosystems (ESA 1991).

Succession, the process of ecosystem change and development, has been a central theme in ecology and the dominant theme in the application of ecology to rangeland management. As early as 1917, it was recognised that knowledge of successional processes was indispensable to managing rangeland (Sampson 1917). Early models of succession viewed ecosystem change as a deterministic process proceeding toward a fixed endpoint, or climax vegetation that was in equilibrium with soils and climate (Clements 1916). If a disturbance occurred that moved the plant community away from climax (retrogression), progress back toward climax (secondary succession) was predictable once the disturbance was removed.

The early work of Dyksterhuis (1949; 1958) provided a conceptual framework for integrating the dominant theory of succession into rangeland management and quantitatively assessing the status of rangeland. Successional status (range condition) was measured by deviation from an hypothesised climax for unique soil and climate combinations (range sites). In addition to the theoretical aspects, his work provided a quantitative basis for evaluating alternatives and monitoring the effects of decisions. This has been, without a doubt, the most influential application of ecology to natural resource management in this century.

Sufficient observational and experimental evidence is now available to invalidate the climaxbased linear succession model as the dominant paradigm of rangeland dynamics (Joyce 1993). However, ecology, and vegetation dynamics in particular, is still the most logical basis for sustainable rangeland management (Whalley 1994). Non-equilibrium ecology has emerged as the dominant theory of ecosystem change (May 1977) — and currently appears to provide the most appropriate framework for explaining observations (Westoby 1980), and thus, providing a foundation for management. The state and transition approach of Westoby et al. (1989) integrates non-equilibrium ecological theory into rangeland management. This approach appears to offer the greatest opportunity to improve the scientific basis of managing rangelands.

The current challenge for scientists is to identify inconsistencies between theory and application and retain or reject the theory. If the theory is retained, the challenge for scientists and managers is to refine the linkages and develop a consistent, logical basis for land use and management decisions. To adequately test the utility of any model an analytical approach is required. A model of ecosystem dynamics that has value to range management must do 4 things:

- provide a means of predicting (at least qualitatively) change among the components of the system;
- provide a basis for detecting changes in relations among the components of rangeland ecosystems before they are irreversibly entrained;
- assist managers to make informed choices among alternatives and initiate actions to achieve objectives; and
- facilitate communication among rangeland researchers, extension officers, users and managers, and the general public.

If non-equilibrium ecology (the theory) and state and transition models (the application) are an adequate basis for rangeland management, these criteria should be largely satisfied. In this paper, I assess the state and transition approach against each of these criteria. The criteria for rejection (non-use) or acceptance (use) will not be absolute, but relative; does it do a better job than what we have now? Although the range condition model (Dyksterhuis 1949) is not used explicitly throughout the world, much of the philosophy that underlies management of extensive grazing relies on a notional climax or pristine state and management oriented to minimise departure from that state. Therefore, the range condition model provides the most suitable comparison.

## Predicting change

Although prediction is only one function of models, it is of paramount importance if informed decision making is the goal (Bellamy and Brown 1994). Accurately predicting change in ecological systems should focus on attributes and processes that organise ecosystems (Cattelino et al. 1979; Noble and Slatyer 1980). The basis

for predicting ecosystem response to natural or human-induced changes is an understanding of the process of succession. Clementsian ecology and the range condition model rely exclusively on competition as the dominant process in secondary succession (Pickett et al. 1987). Models that integrate non-equilibrium ecology into rangeland management focus on multiple ecosystem attributes such as resistance and resilience, temporal thresholds and feedback loops and how they affect the processes of vegetation change (Archer and Smeins 1991; Friedel 1991; Lavcock 1991). The validity of assumptions about organising processes and attributes should provide insight into the ability of the model to predict change accurately.

## Competition

Competition as the organising process in determining community structure has been questioned over the past 2 decades (Drury and Nisbet 1973; Connell and Slatyer 1977; Connell 1983; Schoener 1983). Fowler (1990) described 10 causes of "disorderliness" or the lack of consistency in applying results of competitive outcomes to observed successional patterns. Complexity, spatial and temporal variation, regulation at larger scale, historical effects, and stochastic dispersal of plant propagules are some of those causes that are relevant to rangeland plant communities. In each case, the determinants of competitive outcomes shift from processes that occur at micro-scales to meso- and macro-spatial scales. Inferences about competitive ability drawn from casual observation of plant traits or small plot and population level responses may be irrelevant in predicting community patterns (Brown and Stuth 1993). Therefore, models to predict change based on competition may be inaccurate and misleading.

#### Resistance and resilience

Begon et al. (1990) defined 2 important aspects of ecosystem change — resistance and resilience. Resistance refers to the ability of an ecosystem to absorb disturbance (events that change structure and alter resource availability, Rykiel 1985; Pickett and White 1985) and retain its characteristics. Resilience refers to the ability of an ecosystem to regain its original state after a change has occurred. Although much more

complex and involved attempts have been made to describe aspects of ecosystem integrity (see Kay 1991), resistance and resilience are especially applicable to the use of state and transition models for managing rangeland.

Scholes and Walker (1993) described resistance to change in a southern African savanna with distinct patches dominated by either grasses or shrubs. In patches with a dense cover of perennial grasses (light grazing), soil moisture was pre-empted by extensive root systems of grasses and fuel for fires was abundant. The combination of competition and burning suppressed tree growth. As long as grass cover remained dense, the system was stable and the resistance to conversion to a woodland was high. In patches where grass cover was reduced by heavy grazing or when fire was suppressed, trees dominated. In this case, once trees established, they accessed soil moisture and limited grass growth. In both instances, patches representing each stable state were relatively resistant to change, if the burning and grazing regimes were held constant.

Resilience was illustrated in a relatively simple sown pasture system by Jones (1992). Heavily grazed legume (*Macroptilium atropurpureum* cv. Siratro)–grass (*Setaria sphacelata* cv. Nandi) paddocks were invaded by stoloniferous grasses within 5 years of sowing. Grazing was then permanently excluded on portions of the paddock at 2-yearly intervals over the following 10 years. Areas protected early in the experiment recovered quickly while areas grazed heavily for longer periods before being protected took longer to recover. Areas exposed to 10 years of heavy grazing and then protected did not recover during the experiment.

## Thresholds

As ecosystems change they often pass through thresholds. Thresholds are boundaries in space and time between 2 states and, in general, once a threshold is crossed, it is difficult to return (Friedel 1991). Archer (1989) provides an example in a subtropical savanna in Texas being converted to a shrubland. The invasive shrubs are natives and a persistent component of the ecosystem. However, when conditions are altered, in this case by suspension of fire, small plants with little effect on ecosystem processes gain access to resources and express themselves

(Brown and Archer 1990). Ultimately, the structure and function of the ecosystem resembles that of a shrubland rather than a savanna. Once the transition to shrubland is made, periodic, moderate intensity fire has little effect on adult shrub clusters (Archer 1990). Thus, fire, the disturbance element responsible for maintaining an open savanna, has little effect on restoring a savanna once the threshold to shrubland has been crossed.

Harrington (1991) illustrated a similar phenomenon for NSW rangelands. Although *Dodonaea* shrubs establish infrequently, the combination of reduced grass competition (via overgrazing) and higher than normal precipitation lead to increased seedling success. In addition, suspension of burning increased seedling survival and growth rates. Although the physiognomy remained that of a grassland, processes necessary for change were entrained long before vegetation structure changed. The point at which fire and competition from grasses can no longer exert an influence over woody seedling success represents the conversion threshold for this rangeland ecosystem.

# Ecological feedback

Feedback governs the rate of change in an ecological system (Kitching 1983). Negative feedback has an inhibitory (or stabilising) effect on change while positive feedback has an accelerating (or disruptive) effect. For example, a negative feedback between drought and forage consumption by grazers may be linked to the ability of grasslands to maintain integrity under increased grazing pressure during drought. Forage intake decreases as forage quality declines (Van Soest 1987). When drought limits plant productivity, forage quality also drops to levels that inhibit digestibility (Rao et al. 1973). As a result, forage residence time in the rumen is increased and intake is limited, thereby reducing grazing pressure. This negative feedback suppresses changes in grass species composition associated with heavy grazing.

A potentially disruptive de-coupling of the feedback loop occurs when supplements are provided for grazing animals during the dry period, stimulating intake (e.g. Gardener *et al.* 1990). Increased grazing pressure lowers survival of perennial grasses (Mott *et al.* 1992) and shortlived perennials, annuals and forbs increase.

Positive feedback occurs in the shift from grass to shrub-dominated savanna in southern Africa (Walker and Noy-Meir 1981). The balance between grasses and shrubs is maintained by the ability of each lifeform to preferentially exploit soil moisture at different depths. Although both lifeforms have access to moisture at a range of depths, generally grasses extensively exploit shallow soil layers and shrubs intensively exploit deeper layers. When overgrazing reduces grass root biomass and activity in upper soil layers, moisture percolates into lower soil layers and increases supply to existing shrubs. Enhanced shrub growth increases competition for soil moisture with grasses in the upper soil layers and reduces grass productivity. If stocking rates are not adjusted, further overgrazing occurs, increasing the rate of the process.

Schlesinger et al. (1990) illustrated a positive feedback between livestock grazing and desertification in desert grasslands of North America. When grass cover is reduced by overgrazing, overland flow of water concentrates nutrients and organic matter beneath established shrubs. Subsequently, shrub growth and reproduction increase. The transfer of nutrients and water to shrubs further reduces growth of grasses and groundcover. Thus, the rate of ecosystem change is accelerated.

Many other examples of vegetation change in rangeland ecosystems have illustrated that change is often not linear and recovery from disturbance may follow successional pathways that do not resemble their original development (see Lauenroth and Laycock 1989 for examples). Since state and transition models allow for nonlinear representation of ecosystems, they do offer an improved capacity to predict changes in ecosystem properties compared to the range condition model. Qualitatively expressing thresholds and describing the effect of feedback processes can more easily be incorporated and transition models offer a significant improvement over the existing approach. Just as the original range condition model was never intended to be a quantitative model to describe succession on a given site, the state and transition approach cannot be used to predict ecosystem performance at fine scales (the species composition level). However, mathematical and statistical models that integrate principles of non-equilibrium ecology can be used for quantitative prediction at fine scales (see Scanlan 1994).

# **Detecting change**

The basis of successful rangeland management within the range condition model is matching stocking rate to carrying capacity (Stoddart et al. 1975). The premise is that, if long term stocking rate and carrying capacity are in or near balance, successional status will be advanced and stable (Pieper and Heitschmidt 1988). A second premise is that successionally advanced ecosystems are more efficient in terms of ability to convert inputs to outputs and to conserve and recycle resources (Odum 1969) and are, therefore, more desirable. Thus, monitoring successional status is assumed to provide an indication of how well stocking rate and carrying capacity are balanced and should provide an ability to detect change. Recently, however, the validity of the carrying capacity concept has been questioned as a basis for stocking rate decisions (Bartels et al. 1993). They suggest instead that efforts focus on monitoring system parameters that signal impending undesirable changes as a basis for decision making. If their suggestions are valid, detecting and reacting to relatively major changes in production becomes the most important aspect of range management as opposed to determining initial stocking rates based on average production years and then making minor adjustments in management.

## Community change

In rangeland management, the traditional method of approximating successional status is by comparing extant plant species composition to an hypothesised climax. Succession was generally viewed as a single pathway process in which early successional species modified the environment and facilitated the establishment of more advanced species (Pickett et al. 1987). The underlying assumption is that competition within successionally advanced ecosystems is greater and it follows that species associated with climax communities are the most competitive (Crawley 1986). A proper stocking rate allows climax species to maintain dominance. If grazing is too heavy, competitive ability is diminished and less desirable species dominate. Thus, the impact of grazing in mitigating plant-plant competitive interactions is eventually expressed as successional pattern at the community level and can be measured via changes in species composition.

Monitoring changes in species composition in relation to an assumed climax may be misleading, especially if assumptions concerning competitive ability and interactions with grazing are incorrect (see earlier discussion). Change may be detected, but only after it occurs. In light of this, state and transition models do offer potential for significant improvement in detecting vegetation change within a plant community, if the focus is on proximate causes and mechanisms of change. Techniques to detect change can be developed when processes are identified. However, if the focus is on describing the species composition of various states and co-occurring events, they offer little hope of improvement over the current models.

## Landscape change

Perhaps the most vexing problem in ecology and rangeland management (Coughenour 1991; Levin 1992) has been the difficulty of taking results from observations and experiments conducted at plot and community scales (m<sup>2</sup>) and translating them to management at extensive scales (km<sup>2</sup>). For example, an estimate of forage supply for a paddock derived from plant production data may not be an appropriate guide for setting stocking rate because of the overriding influence of livestock distribution (Sendft et al. 1987). Information collected about the process of plant growth is not directly transferable to the process of livestock grazing in most rangeland situations, because each process is regulated differently (Woodmansee 1990). Plant growth is constrained by moisture, nutrient availability and temperature, while livestock distribution patterns are constrained by topography, condition, water availability, etc.

The discipline of landscape ecology offers potential to improve integration across spatial scales by matching spatial patterns and ecological processes (Turner 1989; Wiens et al. 1993). At the landscape level, each patch in a mosaic has attributes peculiar to that patch, and the magnitude of a process for an entire ecosystem is the sum of patch attributes plus interactions (Remmert 1991). Our ability to exploit any particular ecosystem sustainably will ultimately depend on our ability to manage and detect changes in the interactions as effectively as we manage and detect change in the individual units.

Detecting change at a level appropriate to rangeland management will depend on our ability to link point measurements to landscape processes (see Stafford Smith and Pickup 1993).

In terms of integrating across spatial scales to relevant levels for management, state and transition models are lacking. The information expressed in state and transition models is still largely valid only at the community level. The use of state and transition models as they now stand offers no improvement in scaling community level processes up to landscape level management. However, recent technological advances in remote sensing and computing have opened new opportunities for improvement.

## Relevance to management

While rangeland science and rangeland management are related, they must be viewed as distinct (Provenza 1992). The test of any management model is to integrate the two. A model of ecological dynamics has to be able to integrate prediction and detection of changes in vegetation with economic and social goals and constraints of users in an understandable fashion. The real failure of the range condition model was that it effectively decoupled science from management. Advances in ecological science were not incorporated into management because they were inconsistent with the prevailing model (Svejcar and Brown 1991). In many cases, the goal of improving range condition precluded analysis of the relationship between successional status and other objectives such as livestock performance, water quality and biological diversity (Archer and Smeins 1991). The unquestioned assumption was that they were related. If the objective of using a model is to prove the model works, then there is hardly a need to replace it.

If there is one universal management variable, it is the analysis of costs and benefits. Improving the link between ecology and rangeland management requires linking ecological processes and the costs of manipulating them to financial returns and risk. An ability to array alternative actions, develop goals and objectives and evaluate costs and returns of potential actions is perhaps the greatest improvement in management using state and transition models on rangelands (Filet 1994).

## Communication

Traditionally, management technologies have been developed and transferred primarily to maximise (or optimise) production of an output. One major result of this approach was for research and extension personnel adopting an "intervention" style and concentrating on developing "prescriptions" to solve the problems. Adoption or rejection of prescriptions by land users was generally determined by the degree of agreement in world view among researchers, extension specialists, and potential end-users (Vanclay and Lawrence 1992).

One very difficult task that must be faced up to is that, with a non-equilibrium approach, scientists and extension workers have to stop being "experts" about rangeland management and start focussing on ecosystem processes. Land owners and managers will make their own decisions about desired products, condition of land and operating procedures to achieve objectives. We will be moving from a linear, 2-dimensional world view to a non-linear, multidimensional world view. We may or may not share convictions and ideologies with decision makers, but we do share the ecosystem (Grice and MacLeod 1994). Effective communication should focus on providing information to users in formats that incorporate the most up-to-date information and have the flexibility to allow for non-traditional uses (Carlson and Welch 1993).

In addition to communicating with land users and institutional decision makers, it is very important to communicate with the general public. One very real shortcoming is the inability of professionals to interact with an untrained (in ecology and agriculture) and remote public. The adoption of the state and transition approach will not solve that problem If anything, it will make it more difficult. Substituting a complex model for a simplistic model is not going to solve any communication problems, especially with people that only see natural ecosystems on a 2-dimensional box in their lounges, usually after a long days work replete with their own set of problems. Resource management issues do not adapt well to small screens or quick reports. Unfortunately, people that do get involved at more than a casual level do so because of some emotional motivation (backyard issues). Hence, their understanding of ecological processes is governed by a priori decisions about specific issues and specific circumstances. It will not automatically enhance communication with any user group just because state and transition models more accurately describe the ecosystem. In fact, replacing a linear, 2-dimensional model with a non-linear, multi-dimensional model is clearly a more difficult communication challenge.

#### **Conclusions**

State and transition models do offer some opportunities for improving rangeland management compared with the traditional linear succession model. Since the assumptions that often invalidated linear succession as a basis for management are not present in state and transition models, they offer great potential to improve predictability. If a systems view of change that includes causes, processes, and rates is the basis for developing management models, the chance of success will be increased.

If they are focussed on mechanisms, state and transition models can greatly improve our ability to detect change at the community level. However, they represent little improvement in detecting change at the spatial scales associated with most rangeland-based activities. Detecting change at the landscape scale remains a very real challenge for rangeland management.

Putting research findings into a management context is most likely the greatest value of state and transition models. The framework allows for improved ability to link ecological information with economic costs, returns and risks for management alternatives.

Communicating with rangeland users and the public using state and transition models offers both pitfalls and opportunities. With the improved ability to describe ecosystem dynamics and management interactions, understanding should be enhanced. However, replacing a relatively simple model with a more complex one is a barrier that will have to be overcome. The role of scientists and extension workers as experts must be traded for roles as interactive teachers and sources of reliable information.

The state and transition approach fails to meet fully all of the criteria I have established for acceptance as a working model of rangeland dynamics. However, it is more appropriate than the range condition model and should become the standard. Our job as range scientists and managers is now to test that model and develop more effective models to supplant it.

## References

- ARCHER, S. (1989) Have Southern Texas savannas been converted to woodlands in recent history? American Naturalist, 134, 545-561.
- Archer, S. (1990) Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas USA. *Journal of Biogeography*, 17, 453-462.
- Archer, S. and Smeins, F.E. (1991) Ecosystem level processes. In: *Grazing Management: An Ecological Perspective*. pp. 109-139. (Timber Press: Portland).
- BARTELS, G.B., NORTON, B.E. and PERRIER, G.K. (1993) An examination of the carrying capacity concept. In: Behnke Jr, R.H., Scoones, I. and Kervan, C. (eds) Range Ecology at Disequilibrium. pp. 105-126. (Overseas Development Institute: London).
- BEGON, M., HARPER, J.L. and TOWNSEND, C.R. (1990) Ecology: Individuals, Populations and Communities. (Blackwell: London).
- Bellamy, J.A. and Brown, J.R. (1994) State and transition models for rangelands. 7. Building a state and transition model for management and research on rangelands. *Tropical Grasslands*, 28, 247-255.
- Brown, J.R. and Archer, S. (1990) Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos*, **57**, 366-374.
- Brown, J.R. and Stuth, J.W. (1993) How herbivory affect grazing tolerant and sensitive grasses in a central Texas grassland: integrating plant response across hierarchical levels. Oikos, 67, 291–298.
- CATTELINO, P.J., NOBLE, I.R., SLATYER, R.O. and KESSELL, S.R. (1979) Predicting the multiple pathways of plant succession. *Environmental Management*, 3, 41-50.
- CARLSON, J. and WELCH, B.L. (1993) Strategies for maintenance and restoration of soil, water, flora and fauna resources in cold temperate rangelands. Proceedings of the XVII International Grassland Congress, Palmerston North, 1993. pp. 1779–1783.
- CLEMENTS, F.E. (1916) Plant succession: An analysis of the development of vegetation. *Publication 242. Carnegie Institute of Washington*.
- CONNELL, J.H. (1983) On the prevalence and importance of interspecific competition: evidence from field experiments. *American Naturalist*, 122, 661-696.
- CONNELL, J.H. and SLATYER, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. *American Naturalist*, 111, 1119-1144.
- COUCHENOUR, M.B. (1991) Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate systems. *Journal of Range Management*, 44, 530-542.
- Crawley, M.J. (1986) The structure of plant communities. In: Crawley, M.J. (ed.) *Plant Ecology*. pp. 1-50. (Blackwell Scientific: London).
- Drury, W.H. and Nisbet, I.C.T. (1973) Succession. Journal of the Arnold Arboretum, Harvard University, 54, 331-368.
- DYKSTERHUIS, E.J. (1949) Condition and management of rangeland based on quantitative ecology. *Journal of Range Management*, 2, 104-115.
- Dyksterhuis, E.J. (1958) Ecological principles in plant evaluation. *Botanical Review*, 24, 253-272.
- Ecological Society of America (1991) The sustainable biosphere initiative: an ecological research agenda. *Ecology*, **72**, 371-412.
- FILET, P.G. (1994) State and transition models for rangelands.

  3. The impact of the state and transition model on grazing lands research, management and extension: A review. Tropical Grasslands, 28, 214-222.
- FOWLER, N.L. (1990) Disorderliness in plant communities: comparisons, causes and consequences. In: Grace, J.B. and Tilman, D. (eds) *Perspective on Plant Competition*. pp. 291-306. (Academic Press: New York).

- FRIEDEL, M.H. (1991) Range condition assessment and the concept of thresholds: a viewpoint. *Journal of Range Management*, 44, 422-426.
- GARDENER, C.J., McIvor, J.G. and WILLIAMS, J. (1990) Dry tropical rangelands: solving one problem and creating another. In: Saunders, D.A., Hopkins, A.J.M. and How, R.A. (eds) Australian Ecosystems: 200 Years of Utilization, Degradation and Reconstruction. pp. 279–286. (Surrey, Beatty & Sons: Chipping Norton).
- GRICE, A.C. and MACLEOD, N.D. (1994) State and transition models for rangelands. 6. State and transition models as aids to communication between scientists and land managers. *Tropical Grasslands*, 28, 241–246.
- HARRINGTON, G.N. (1991) Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology*, 72, 1138-1149.
- JONES, R.M. (1992) Resting from grazing to reverse changes in sown pasture composition: application of the state and transition model. *Tropical Grasslands*, 26, 97-99.
- JOYCE, L.A. (1993) The life cycle of the range condition concept. Journal of Range Management, 46, 132-138.
- KAY, J.J. (1991) A nonequilibrium thermodynamic framework for discussing ecosystem integrity. *Environmental Manage*ment, 15, 483-495.
- KITCHING, R.L. (1983) Systems Ecology: An Introduction to Ecological Modelling. (University of Queensland Press: St Lucia).
- LAUENROTH, W.K. and LAYCOCK, W.A. (1989) Secondary Succession and the Evaluation of Rangeland Condition. (Westview Press: Boulder).
- LAYCOCK, W.A. (1991) Stable state and thresholds of range condition on North American rangelands: A viewpoint. Journal of Range Management, 44, 427-433.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967.
- MAY, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269, 471-477.
- McCown, R.L. and WILLIAMS, J. (1990) The water environment and implications for productivity. *Biogeography*, 17, 513-520.
- MOTT, J.J., LUDLOW, M.M., RICHARDS, J.H. and PARSONS, A.D. (1992) Effects of moisture supply in the dry season and subsequent defoliation on persistence of the savanna grasses Themeda triandra, Heteropogon contortus and Panicum maximum. Australian Journal of Agricultural Research, 43, 241-260.
- Noble, I.R. and Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, 43, 5-21.
- ODUM, E.P. (1969) The strategy of ecosystem development. Science, 164, 262-270.
- Pickett, S.T.A. and White, P.S. (1985) Patch dynamics: a synthesis. In: Pickett, S.T.A. and White, P.S. (eds) *The Ecology of Natural Disturbance and Patch Dynamics*. pp. 371-384. (Academic Press: New York).
- PICKETT, S.T.A., COLLINS, S.L. and ARMESTO, J.J. (1987) Models, mechanisms and pathways of succession. *Botanical Review*, 53, 335-371.
- PIEPER, R.D. and HEITSCHMIDT, R.K. (1988) Is short-duration grazing the answer? *Journal of Soil and Water Conservation*, 43, 133-137.
- Provenza, F.D. (1992) Viewpoint: range science and range management are complementary but distinct endeavors. Journal of Range Management, 44, 181-183.
- RAO, W.R., HARBERS, L.H. and SMITH, E.F. (1973) Seasonal change in nutritive value of bluestem pastures. *Journal of Range Management*, 26, 419-422.

- REMMERT, H. (1991) The mosaic-cycle concept of ecosystems— an overview. In: Remmert, H. (ed.) *The Mosaic-Cycle Concept of Ecosystems*. pp. 1–21. (Springer Verlag: New York).
- RYKIEL, E.J. (1985) Towards a definition of ecological disturbance. Australian Journal of Ecology, 10, 361-365.
- SAMPSON, A.W. (1917) Succession as a factor in range management. *Journal of Forestry*, 15, 593-596.
- SCANLAN, J.C. (1994) State and transition models for range-lands. 5. The use of state and transition models for predicting vegetation change in rangelands. *Tropical Grasslands*, 28, 229-240.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. and Whitford, W.G. (1990) Biological feedbacks in global desertification. *Science*, 247, 1043-1048.
- Schoener, T.W. (1983) Field experiments on interspecific competition. *American Naturalist*, 122, 240-285.
- SCHOLES, R.J. and WALKER, B.H. (1993) An African Savanna: Synthesis of the Nylsvley Study. (Cambridge University Press: Cambridge).
- SCIFRES, C.J. (1987) Decision-analysis approach to brush management planning: ramifications for integrated range resources management. *Journal of Range Management*, 40, 482-490.
- SENDFT, R.L., COUGHENOUR, M.B., BAILEY, D.W., RITTEN-HOUSE, L.R., SALA, O.E. and SWIFT, D.M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience*, 37, 789–799.
- STAFFORD SMITH, M. and PICKUP, G. (1993) Out of Africa, looking in: Understanding vegetation change. In: Behnke Jr, R.H., Scoones, I. and Kervan, C. (eds) Range Ecology at Disequilibrium. pp. 196-226. (Overseas Development Institute: London).
- Stoddart, L.A., Smith, A.D. and Box, T.W. (1975) Range Management. (McGraw-Hill: New York).
- SVEICAR, T.J. and BROWN, J.R. (1991) Failures in the assumptions of the condition and trend concept for management of natural ecosystems. *Rangelands*, 13, 165-167.
- TURNER, M.G. (1989) Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics, 20, 171-197.
- VAN SOEST, P.J. (1987) Evolution and the role of the ruminant. In: Van Soest, P.J. (ed.) Nutritional Ecology of the Ruminant. pp. 1-13. (Cornell University Press: Ithaca).
- Vanclay, F. and Lawrence, G. (1992) Farmer rationality and the adoption of environmental sound practices: a critique of the assumptions of agricultural extension. *Proceedings* of the Annual Meeting of the Rural Sociological Society.
- WALKER, B.H. and NOY-MEIR, I. (1981) Aspects of the stability and resilience of savanna ecosystems. In: Huntley, B.J. and Walker, B.H. (eds) Ecology of Tropical Savannas. pp. 556-590. (Springer Verlag: New York).
- WESTOBY, M. (1980) Elements of a theory of vegetation dynamics in arid rangelands. Israel Journal of Botany, 28, 169-194
- Westoby, M., Walker, B.H. and Noy-Meir, I. (1989) Opportunistic management for rangelands not at equilibrium. Journal of Range Management, 42, 266-274.
- WHALLEY, R.D.B. (1994) State and transition models for rangelands. 1. Successional theory and vegetation change. *Tropical Grasslands*, 28, 195-205.
- WIENS, J.A., STENSETH, N.C., VAN HORNE, B. and IMS, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, 66, 369-380.
- WOODMANSEE, R.G. (1990) Biogeochemical cycles and ecological hierarchies. In: Zonneveld, I.S. and Forman, R.T.T. (eds) Changing Landscapes: An Ecological Perspective. pp. 57-71. (Springer-Verlag: New York).