Archer, S, CJ Stokes. 2000. Stress, disturbance and change in rangeland ecosystems, pp. 17-38. *In:* **Rangeland Desertification** (O Arnalds and S Archer, eds). Advances in Vegetation Science Vol. 19, Kluwer Publishing Company.

Stress, disturbance and change in rangeland ecosystems

Steve Archer and Chris Stokes
Department of Rangeland Ecology & Management, Texas A&M University, College Station, TX 77843-2126, USA
Tel: 409 845 7332; Fax: 409 845 6430; E-mail: <sarcher@vms1.tamu.edu> & <cstokes@tamu.edu>

ABSTRACT Ecological systems and the organisms which comprise them have evolved with and are a product of various stresses, perturbations, and disturbance regimes. However, in human-influenced systems, new disturbances and stresses may be introduced and the frequency, intensity and spatial extent of natural disturbances altered. Natural and anthropogenic disturbances invariably co-occur, so it becomes difficult to ascertain which may be the proximate cause of ecosystem change. It is likely that their effects are compounded by synergistic interactions. In some cases, anthropogenic disturbance may alter the susceptibility of organisms, populations and communities to natural disturbances. In other cases, anthropogenic activities may initiate positive feedbacks that produce rapid, unexpected changes in ecosystem structure and function. These changes may be stabilized by new ecosystem processes, making them irreversible over time frames relevant to management.

An understanding of stress and disturbance will help resource managers to (1) mitigate anthropogenic disturbances which might threaten sustainability and lead to undesirable and potentially irrevocable changes in ecosystem processes and (2) increase chances for success in rehabilitating or restoring degraded ecosystems. Here, we review the role of stress and disturbance in regulating the structure and function of rangeland ecosystems, and present conceptual models of ecosystem change which result from alterations of disturbance regimes. We then discuss rates and dynamics of change and present examples which illustrate how anthropogenic alteration of natural disturbance regimes can alter ecosystem stability and produce multiple stable states. We conclude with a brief discussion of land degradation from ecological vs. socio-economic perspectives.

Key words: degradation, feedbacks, resilience, stability, thresholds, transitions.

1. INTRODUCTION

Degradation and desertification processes are typically associated with arid and semi-arid regions. However, this represents a rather narrow view moves grass biomass aboveground and curtails root production belowground. If maintained at high intensity for sufficiently long periods, grazing can lead to a loss of plant cover, shifts in species composition, erosion or volatilization losses of soil nutrients, and the elimination of natural disturbances such as fire. A disturbance regime is the sum of types, frequencies and intensities of disturbance through time in the landscape. Frequent, small-scale disturbances, such as those resulting from patch grazing, wallowing, and urine and dung deposition by herbivores contribute to the development of fine-grained mosaics across landscapes which may experience infrequent fire and rare, but recurring, drought which affect the entire landscape and watershed. Interpreting ecosystem structure and function is thus contingent upon understanding the interactive role of concurrent, multiple-scale disturbances (Collins and Barber, 1985; Loucks et al., 1985; Chapin et al., 1987; Collins, 1987).

Disturbances are generally perceived as negative, because they are accompanied by elements of damage. However, a disturbance at one level of organization does not necessarily induce change if it is 'absorbed' at higher levels of ecological organization. Disturbance can therefore be viewed as part of the internal workings of an ecosystem rather than as exogenous events (see Ludwig and Tongway, this volume). Indeed, some level of disturbance may be necessary for maintenance of ecosystem properties. Savanna landscapes, for example, are often stable despite consisting of numerous patches in various states of transition between grass and tree dominance caused by grazing, browsing and fire (Dublin et al., 1990; Scholes and Archer, 1997).

Perturbations can be viewed as the response of an ecological component or system to disturbance, as indicated by deviations relative to a specified reference condition (Rykiel, 1985). Perturbations are transient if the system returns to its original steady state or permanent if they lead to a deviation which becomes fixed and produces a steady state different from the original.

Stresses are specific factors that adversely affect the physiology or function of organisms and ecosystems. Factors which alter resource availability or which push resource modulators such as temperature to extremes induce stress. Stresses which result from disturbance or weather may be chronic (relatively continuous, but at low levels) or acute (having a rapid onset and followed by a short, but severe effect) and may either impair function or cause mortality. Stresses do not typically occur in isolation (Chapin et al., 1987).

3. DISTURBANCE, CLIMATE AND STRESS INTERACTIONS

Disturbances are superimposed on a background of topoedaphic heterogeneity and climatic variability. As a result, plant species whose adaptations to the prevailing climate and soils would make them the competitive dominants of the community under one disturbance regime, may assume subordinate roles or even face local extinction when disturbance regimes change. Disturbances such as fire, flooding, and pathogen outbreaks may be directly or indirectly related to climate (e.g., Swetnam and Betancourt, 1990).

In many instances it is difficult to determine the extent to which climate change and disturbance are responsible for driving ecosystem changes (Herbel et al., 1972; Chew, 1982; McNaughton, 1983; Branson, 1985; Foran, 1986; Verstraete, 1986). The difficulty in making this distinction is, in part, due to the fact that shifts in vegetation may lag well behind the climatic changes that drive them. For example, it has been hypothesized that the desert grassland vegetation of the Chihuahuan Desert recorded by settlers of North America in the late 1800s, established under and adapted to 300 years of cooler, moister climates of the 'Little Ice Age' and is only marginally supported under the present climate (Neilson, 1986). If this hypothesis is correct, climate-driven 'desertification' of these grasslands and their replacement by desert scrub may have been in progress at the time of Anglo-European settlement, and augmented, but not caused, by anthropogenic alteration of grazing and fire regimes.

Disturbance and climate can interact to offset or reinforce ecosystem change. Disturbance effects may be minimal when climatic conditions are favorable or magnified when climatic conditions are extreme. Anthropogenic activities may reinforce or accelerate changes triggered by natural events. For example, grassland retrogression associated with livestock grazing may be mitigated in years of normal or above-normal rainfall and magnified during years of below-normal precipitation (Herbel et al., 1972; Clarkson and Lee, 1988; O'Connor, 1993; Orr et al., 1993; O'Connor, 1994). The encroachment of unpalatable trees and shrubs into grazed subtropical grasslands and savannas illustrates the potential for interaction between climate and grazing disturbance (Fig. 2). In this case, woody plant cover decreased slightly between 1941 and 1960, apparently the result of a major drought during the 1950s. In the subsequent pluvial period, woody plant cover increased 2- to 4-fold. Changes in ecosystem structure have therefore been punctuated and abrupt rather than gradual and continuous. Drought may have predisposed the system to rapid rates of woody plant invasion in the post-drought period. However, these sites had also been heavily grazed by cattle since the mid-1800s. Cattle effectively disperse seeds of the dominant woody plant and it is likely that their utilization of grasses intensified drought stresses on these plants. Continued post-drought grazing would also have limited the mass and continuity of fine fuels needed to carry fire. Livestock grazing could thus contribute significantly to woody plant expansion. Would either drought or livestock grazing alone have been sufficient to produce this pattern and magnitude of change? It is likely that these changes were the result of the combined effects of these two disturbances acting together. Thus, certain changes in environmental conditions may be necessary, but they are not sufficient by themselves to elicit a change in ecological systems.

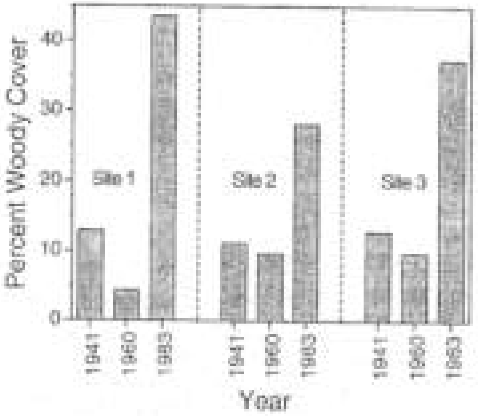

Figure 2. Changes in landscape cover of woody vegetation in a subtropical savanna parkland between 1941 and 1983 (from Archer et al., 1988). This site has a history of heavy, continuous grazing by cattle and experienced a major drought during the 1950s. It is likely that drought and grazing combined to affect the dynamics of bush encroachment in a way that neither factor operating independently would have. See also Case III in Fig. 6.

Disturbances serve to overcome vegetation inertia by lessening the dominance of established plants and creating opportunities for new plants which may be better adapted to the present climatic conditions. Ecosystem simulations indicate that climate change alone may have a minimal short-term influence on composition. For example, in simulations by Overpeck et al. (1990), the response of forest vegetation to climate change took >200–250 years to achieve equilibrium in the absence of disturbance. By contrast, vegetation subjected to disturbance closely tracked the initiation and timing of climate change and produced a vegetation with novel and unique characteristics.

4. MULTIPLE STEADY STATES, TRANSITION THRESHOLDS AND POSITIVE FEEDBACKS

Once ecosystem change has occurred, relaxation of stress and disturbance or an improvement of environmental conditions will not necessarily enable a system to return to its previous state (c.f., Rapport and Whitford, 1999). Alteration of soil structure (Thurow, this volume), distribution and abundance of water and nutrients (Ludwig and Tongway, this volume; Havstad et al., this volume; Tongway and Hindley, this volume), and plant composition (Hobbie, 1992) may occur and re-direct ecological processes and stabilize the site in a new steady-state arrangement. This suggests the existence of critical transition thresholds. Stochastic, climatic events may hasten disturbance-mediated transitions (e.g., O'Connor, 1993). Transitions may be further accelerated if "keystone species" establish and initiate positive feedbacks to redirect succession or change disturbance regimes (Archer et al., 1988; D'Antonio and Vitousek, 1992).

How far can ecological systems be pushed before crossing the line of ecological function that separates one steady-state from another? Are contrasting ecosystem states endpoints of a continuum of steady, continuous change? Or, is a given ecological state relatively stable over a range of disturbance regimes and environmental conditions, but then prone to radical change when these ranges are exceeded? The former implies gradual, incremental change; the latter a highly discontinuous behavior. As suggested in the following examples, both are likely to occur and their relative importance is often a matter of perspective (see also Fig. 4 in Tongway and Hindley, this volume). Detection and definition of thresholds will depend on values attached to signal and noise in ecological processes, the spatial and temporal frames of reference, the purpose behind studying ecosystem change, and the indicators used to quantify ecosystem condition and variation.

4.1 High latitude example

Desertification of Icelandic rangelands has been extensive and spectacular (A. Arnalds, 1987; O. Arnalds, this volume). The degradation process (Figs. 3 and 4) appears to begin when unregulated livestock grazing shifts vegetation from a continuous cover of palatable deciduous shrubs, grasses and forbs (State I) to less productive heathland dominated by unpalatable evergreen dwarf shrubs and forbs (State II) (Aradottir et al., 1992). Reduction of the plant biomass thermal barrier makes soils more prone to frequent small-scale disturbances associated with frost boils and frost heaving. This hastens the formation of bare patches, which expose the friable, thick (50–200 cm) mantle of volcanic soil (State III). The exposed soil mantle is then removed by wind and water erosion (O. Arnalds, 1998). As these eroded patches enlarge and coalesce, the length of exposed, eroded perimeter increases dramatically, creating 'erosion fronts' whose vertical faces (rofabards) are fully exposed to wind (O. Arnalds, 1990, 1999). These elongated, wind-driven fronts can now advance rapidly across the landscape, leaving an infertile soil surface in their wake. Management of the remaining vegetated zones does little to prevent the advance of the erosion fronts. Self-reinforcing changes now occur very rapidly (States III and IV), culminating in a landscape characterized by either glacial till or sandy surfaces with widely scattered vegetated remnants (States V and VI).

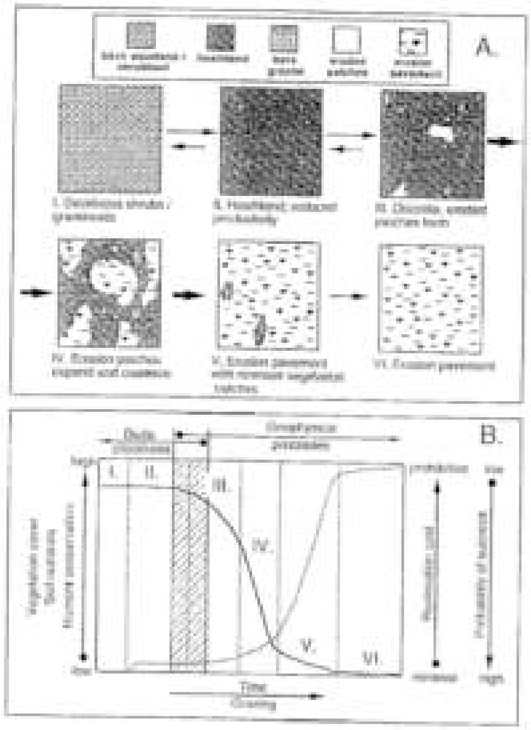

Figure 3. Degradation of birch woodlands in Iceland (adapted from Aradottir et al., 1992). (A) Changes in land cover status brought about by grazing and erosion. (B) Conceptual model of the dynamics of change in land cover status (solid line) and associated restoration costs (dashed line). (For further elaboration see Figs. 3 and 4 in Tongway and Hindley, this volume).

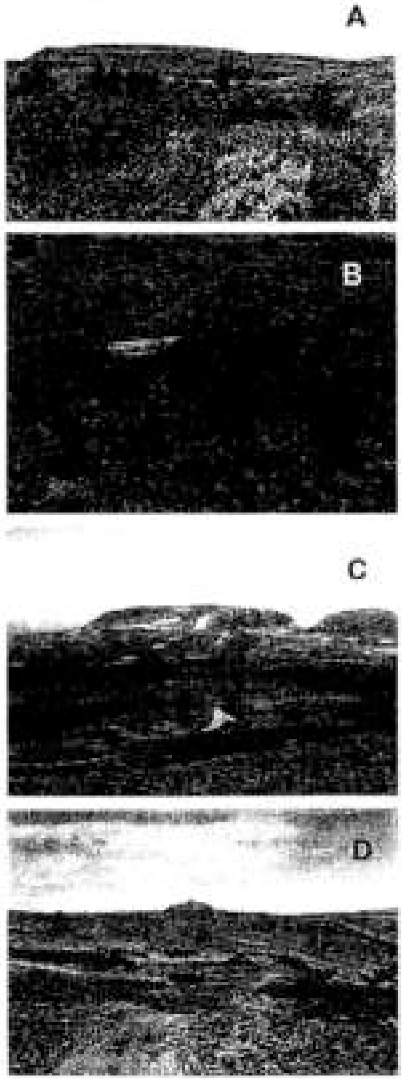

Figure 4. Icelandic landscape states represented in Fig. 3. (A) Birch (*Betula pubescens*) shrubland typical of areas protected from sheep grazing; (B) Heathland vegetation associated with grazed areas. Note bare ground patches. These sites are now increasingly destabilized by frost heaving and are subject to wind/water erosion (C) Erosion escarpments (rofabards) that move rapidly across the landscape regardless of vegetative cover. (D) Glacial till and remnant soil. Aeolian deposition of soils from these sites create active dunes that bury vegetation and soils on other sites.

Changes appear to be rather gradual and continuous from State I to State II. Soil structure, fertility, plant cover and biotic processes which modulate climate and nutrient fluxes are still in place. Thus, relaxation of grazing and progressive intervention may permit a return to State I. The system at State I may also be resistant to environmental stresses, such as unusually cold growing seasons or tephra deposition associated with volcanic activity. However, in State II, these same stresses may push the system past a threshold, propelling it to states of advanced degradation. For landscapes in State III, relaxation of grazing (i.e., removal of disturbance) may be of little consequence, because geophysical processes (frost heaving and erosion) alone are driving the system. State VI is highly stable and characterized by geophysical forces and ecological processes very different from those in preceding states. Once in these degraded states, management and restoration options are expensive to implement and have a high probability of failure.

4.2 Semi-arid savanna example

In the Icelandic example, interactions between livestock grazing and environmental events initiate a chain of events leading to a total loss of vegetative cover and massive erosion. In cool and warm temperate arid zones, replacement of grasses by unpalatable shrubs, also potentially initiated by grazing, may cause a redistribution of nutrients and an overall loss of primary and secondary productivity (Kieft et al., 1998; Havstad et al., this volume). These examples contrast starkly with land degradation in sub-humid tropical and subtropical regions, as described in the ensuing paragraphs. Even so, conceptual models of vegetation change based on resilience and thresholds appear applicable.

Numerous quantitative assessments corroborate historical observations which indicate that many regions of North and South America, Africa and Australia were characterized by grasslands and savannas at the time of Anglo-European settlement. Many such areas are now woodlands or shrublands, dominated by unpalatable trees and shrubs (reviewed by Archer, 1994, 1996). These changes in vegetation cover are widely regarded as degradation from a socioeconomic perspective because they have reduced the potential of the land for livestock production.

In semi-arid and sub-humid grasslands and savannas, tall and mid-height grasses are typically the competitive dominants under light grazing; woody plant density is low and grass competition and periodic fire suppress their recruitment. Short-statured grasses are more tolerant to defoliation than the taller grasses or are less preferred. As a result, they increase in abundance with intensification of grazing (Archer and Smeins, 1991). Even so, ground

cover remains high, soils and microclimate are relatively unaffected, and the amount and spatial distribution of fine fuels permits natural or prescribed fire in many years. With relaxation of grazing, taller grasses regain dominance of the site via regeneration from seed or vegetative propagules (Fig. 5).

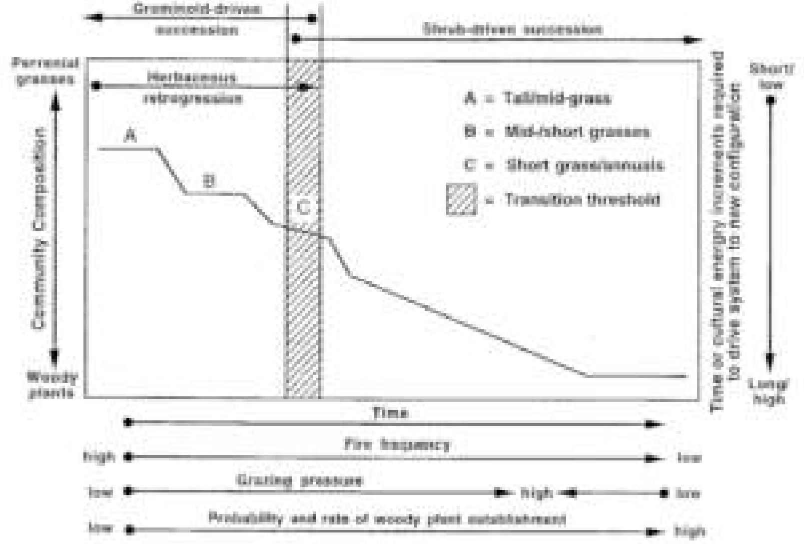

Figure 5. Conceptual model of 'thicketization' (Fig. 1) and transition thresholds in a semi-arid, subtropical savanna (from Archer, 1989). The goal of research should be to characterize plant population or edaphic properties that may forecast impending transitions. The goal of management should be to adjust land use practices to avert crossing thresholds leading to undesirable and potentially irreversible changes in vegetation or soils. (See also Tongway and Hindley, this volume; Ludwig and Tongway, this volume).

With continued intensification of grazing, perennial short-grasses are replaced with annuals and weakly perennial grasses of low litter and nutrient quality. Bare ground increases and promotes warmer, drier microclimates and wind or water erosion (Thurow, this volume). Fire may be virtually eliminated, as there is seldom sufficient fine fuel for ignition and spread (Baisan and Swetnam, 1990; Savage and Swetnam, 1990). Unpalatable N_2-fixing or evergreen shrubs adapted to the harsher microclimate and low nutrient environments may now establish. As woody plant density increases, herbaceous production declines further, thus increasing the grazing pressure on remaining herbaceous patches. By this time, a physiognomic or domain threshold has been crossed, whereby soils, seedbanks and vegetative regenerative potentials have been modified such that succession will now progress toward shrubland or woodland even if grazing pressure is relaxed. The system has therefore moved from a grassland domain to a shrubland or woodland domain. Drought, natural disturbance, or anthropogenic manipulation (chemical/mechanical brush management practices) may open up woody plant canopies and enable grass production to increase temporarily. However, woody plants quickly regain dominance of the site via seed or vegetative propagation (Scifres et al., 1983; Fulbright and Beasom, 1987; Whitford et al., 1995). At this point, bush clearing may be neither economically feasible nor ecologically sound.

Data from savannas of the Edwards Plateau of central Texas, USA appear to exemplify this grassland-to-woodland transition. This region has been heavily and continuously grazed by livestock since the mid-1800s. In 1948, a long-term stocking rate manipulation experiment was initiated to quantify grazing impacts. On sites where grazing was relaxed and excluded, cover of unpalatable evergreen shrubs increased 2– to 4–fold by 1983 (Smeins and Merrill, 1988). Such data suggest that by the time progressive livestock management practices were implemented in 1948, these systems were already in the woody plant 'domain of attraction.' As a result, relaxation of grazing had little bearing on the system's inertia towards woody plant domination.

5. CONCEPTUAL MODELS OF ECOSYSTEM CHANGE

Traditional 'retrogression sequence' models have dealt with single transitions involving responses to particular disturbance regimes (e.g., Dyksterhuis, 1949; Bosch and Booysen, 1992). These models have been continually refined to deal with inadequacies in the successional theory on which they were originally based (Connell and Slatyer, 1977; Archer, 1989; Luken, 1990; Friedel, 1991; Laycock, 1991; Joyce, 1993). Another approach has been to consider the responses of ecosystems to different sets of stress and disturbance regimes and the alternate ecosystem states that result from these transitions (George et al., 1992; Jones, 1992; Milton and Hoffman, 1994). These 'state and transition' (S&T) models have also been useful for understanding the dynamics of vegetation mosaics in highly stochastic environments (Westoby et al., 1989b; Hobbs, 1994; Hoffman, this volume).

State and transition models have gained wide support, but also have limitations (Watson et al., 1996). The definitions of states are typically descriptive 'black boxes' and our understanding of the factors conferring stability within a state or of factors triggering transitions between states is limited. Similarly, the rates and dynamics at which a system moves from one state to another are seldom known. Here, we elaborate a conceptual framework for exploring the dynamics of transitions between states (i.e., the 'arrows' in S&T diagrams).

Long-term, sustained stresses such as grazing can act as directional forcings for gradual, incremental state transitions. However, episodic (rare, but recurring) perturbations in stochastic environments can produce rapid transitions with unpredictable outcomes. Although dogma from dryland systems has emphasized 'event-driven' change, gradual, continuous changes may also be of comparable importance (Watson et al., 1997a,b). Both episodic and continuous changes are therefore of potential consequence. When stresses exceed the buffering capacity of the system, there will be a net imbalance between degenerative and regenerative processes (disequilibrium) leading to a deviation from the initial ecosystem state. These stresses may be natural or anthropogenic. The synergistic interactions of excess stresses and intrinsic disturbance regimes can be conceptualized as a 'pump and valve' system. Periodic environmental stress and disturbance act as a pump for ecosystem change. Unbalanced stresses then act as 'valves' that may favor degenerative changes over processes of regeneration. The greater the stress, the greater the potential for rapid, discontinuous change triggered by stochastic, abiotic forces (e.g., Lockwood and Lockwood, 1993).

There are several mechanisms by which chronic and episodic stress and disturbance may interact to cause degradation (Fig. 6). These are ranked in order of increasing severity for degenerative ecosystem change (or, conversely, increasing desirability for processes of restoration and 'positive' ecosystem change) and increasing potential to cause a transition across a threshold between ecosystem states:

- **Steady-state fluctuations (no excess stress):** In a 'healthy' ecosystem, which is not experiencing excess additional stresses, negative feedbacks maintain a steady state as environmental conditions (e.g., rainfall variability) oscillate around a long-term mean. Perturbations are fully buffered by biotic recovery processes. Fluctuations in ecosystem condition occur, but there is no net deviation from the steady state over the long-term. The ecosystem can be considered to be in dynamic equilibrium with its associated disturbance regime (at a spatiotemporal scale that encompasses fluctuations and patch dynamics).
- **Degradation I (suppressed regeneration):** The effects of additional stresses (such as increased grazing pressure) may not be evident during unfavorable periods. Instead, they may act by limiting the potential for recovery during the regenerative phase of ecosystem fluctuations. Ecosystem structure may be relatively intact, but rates of functional processes may be slowed. For example, as soil properties (Thurow, this volume), seed production, vegetative regeneration or the seed bank are impacted,

system resilience is diminished. Full recovery, therefore, becomes increasingly unlikely, even with removal or alleviation of stresses. Some models of succession make allowance for the effects of disturbance in suppressing successional 'repair' processes (Schlatterer, 1989; Luken, 1990). This form of degradation is common where rangelands are being managed 'on the edge' of sustainability, with the goal of maximizing utilization and off-take. These levels of utilization may appear to be sustainable under 'average' climate conditions or during long runs of favorable years, but gradually deplete the reserve resources required to recover from periods of unfavorable conditions.

- **Degradation II (accentuated degeneration)**: In this scenario, the added stresses act to directly advance degenerative processes. The stresses exaggerate the impacts of adverse environmental conditions (e.g., drought) to the extent that the perturbations cannot be fully counteracted by processes of regeneration in the ensuing favorable period. This is the most basic concept of degradation, where the synergistic effects of natural and anthropogenic stresses overwhelm the ecosystem's buffering capacity.
- **Degradation III (degenerative 'recovery')**: In some cases, effects of the modified stress and disturbance regime may only be expressed during favorable periods. For example, disturbance may enable establishment of undesirable species whose recruitment is subsequently promoted during favorable periods. Or, preferential utilization of plants by livestock may reduce seed production or vegetative regeneration of desirable species, while enhancing that of unpalatable species (Milton, 1992; Stokes, 1994). Favorable periods of vegetation regeneration would then be biased to recruitment of the unpalatable species (see also Fig. 2). Undesirable states thus develop and are reinforced, becoming increasingly favored over time as a positive feedback develops. In the worst cases, positive feedbacks would be established in which the delayed response would continue long after the inducing stresses had been alleviated. This would indicate the crossing of a physiognomic or domain threshold with potentially irreversible changes to the ecosystem (Fig. 5). Establishment of species that change the disturbance regime can also initiate these undesirable positive feedbacks. Exotic grasses, for example, can increase fine fuel loads and hence the probability of fire. Favorable environmental periods enhance their establishment and biomass accumulation, thus increasing fire frequency and intensity to further promote their spread into new habitats (D'Antonio and Vitousek, 1992). Positive feedbacks dominated by abiotic processes (e.g., Icelandic example; Figs. 3 and 4) are potentially more devastating than positive feedbacks dominated by biotic processes (e.g., 'thicketization' of savannas; Figs. 2, 5 and 7). Biotic positive feedbacks may lead to a change in ecosystem composition and function, whereas abiotic positive feedbacks are often accompanied by nudation and loss of basic ecosystem functions (e.g., nutrient cycling).

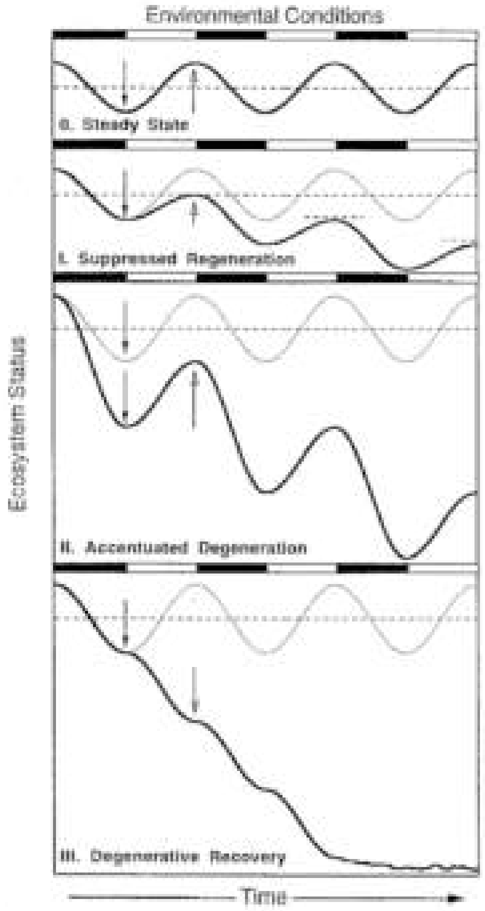

Figure 6. Conceptual model of ecosystem degradation in conjunction with climatic and environmental fluctuation. Dark arrows denote degenerative changes that occur during stressful environmental periods (solid segments of x-axis); clear arrows denote regenerative changes occurring during favorable environmental periods (clear segments on x-axis). Rates and dynamics of directional change (retrogression, degradation) are influenced by climatic variability and may be caused by dampening of recovery processes (Case I), accentuation of stress levels (Case II) and regeneration that is biased towards recruitment of undesirable species during favorable periods (Case III).

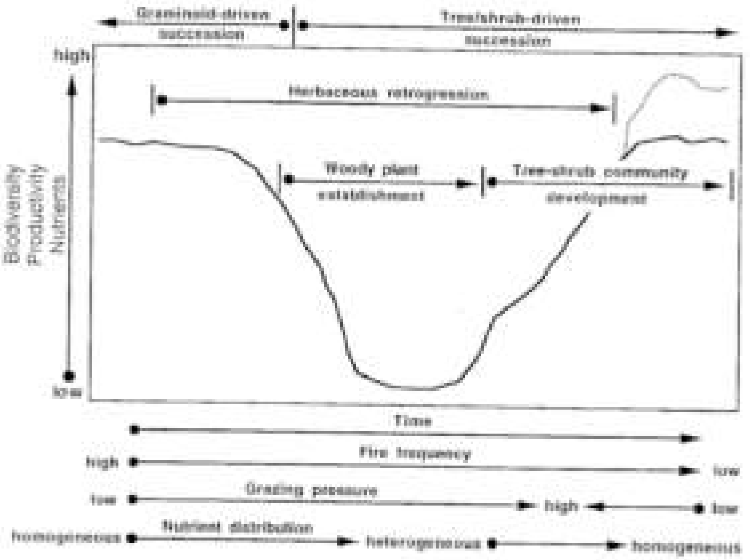

Figure 7. Conceptual model of ecosystem changes associated with 'thicketization' of a semi-arid, subtropical savanna parkland. Degradation associated with grazing-induced herbaceous retrogression leads to the establishment of productive, but unpalatable woody plants (Figs. 2 and 5). The productivity, biodiversity, plant/soil nutrient capital in the woodlands which subsequently develops may meet or exceed that of the original ecosystem. Ecological degradation may therefore be transient. The woodland landscapes are typically regarded as 'degraded' from a socioeconomic perspective, because their capacity for cattle production, the historical use of these lands, has diminished. (See also Tongway and Hindley, this volume).

6. ANTICIPATING CHANGE

State and transition models have provided a useful framework for highlighting critical events that create management hazards (unfavorable transitions) and opportunities for intervention (conditions for favorable transitions) (Westoby et al., 1989a). We now need a better quantitative and mechanistic understanding of why these transitions occur and how biotic and abiotic factors interact to promote or discourage them. From an applied perspective, we need to clarify how management actions before, during and after critical events might alter transition probabilities. A better understanding of transition mechanisms will also help identify and clarify key monitoring variables. Important changes that affect system response to perturbation events may go undetected unless variables with appropriate sensitivity are monitored (Stokes, 1994). Thus, there is an important need to develop sensitive indicators that can give advance warnings, so that ecosystem management can be adjusted to minimize the likelihood of undesirable transitions or to promote desirable transitions.

7. DEGRADATION: ECOLOGICAL OR SOCIOECONOMIC?

Degradation associated with 'desertification' in arid environments (e.g., Schlesinger et al., 1990; Rapport and Whitford, 1999; Havstad et al., 1999) or 'deforestation' in humid environments (Figs. 3 and 4) are a sharp contrast to that associated with the 'thicketization' of grasslands and savannas in more mesic environments. The former have negative consequences both ecologically and socioeconomically. Thicketization may have adverse socioeconomic implications, as it reduces the capacity of rangelands for subsistence or commercial livestock production. However, it does not necessarily represent a degraded system with respect to ecological characteristics such as biodiversity, productivity, or plant/soil nutrient capital.

The conceptual model in Fig. 7 indicates that a degradation phase may be followed by a reconstruction phase which begins when unpalatable woody plants establish, grow, modify microclimate and enrich soil nutrients. Dynamic simulations in subtropical savanna parklands in southern Texas support this conceptual model and indicate that degradation of grassland occurred subsequent to intensification of livestock grazing in the mid-1800s. This was manifested as a significant decline in primary productivity and plant/soil carbon and nitrogen pools. However, with selective grazing and the elimination of fire, nitrogen-fixing woody plants invaded, ameliorated microclimatic conditions, enriched soil nutrient pools and facilitated the establishment of a diverse assemblage of herbaceous dicots and shrubs (Archer, 1995). Present-day landscapes are a rich mosaic of productive woodlands and tree-shrub patches interspersed with remnant grass-dominated patches. It is estimated that current plant and soil C and N mass is substantially greater than that which occurred under 'pristine' conditions (Hibbard, 1995). In addition, these landscapes are highly resilient following severe disturbance (Flinn et al., 1992; see also Whitford et al., 1995) and are regarded as excellent habitat for numerous wildlife species, both game and non-game. So, in this case, the system which has developed following an initial degradation phase is now ecologically productive and diverse. It would seem that it is 'degraded' only with respect to its socioeconomic value for cattle grazing. However, it has other potential socioeconomic values that necessitate a change from traditional uses. These include alternate classes of livestock (e.g., goats), lease hunting and ecotourism.

8. CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Early successional models of rangeland degradation probably encouraged overly optimistic attitudes towards rangeland management, especially with respect to the potential for rangelands to recover from excessive utilization. However, for the past decade, there has been growing acceptance that anthropogenic disturbances often produce altered vegetation states that are stable enough to make the changes practically irreversible (Natural Resources Council, 1994; Rapport and Whitford, 1999). Widespread observations indicate that once critical disturbance thresholds are crossed, degradation of the structure and function of rangelands will not necessarily be halted or reversed simply by decreasing or removing anthropogenic stresses. In rangelands where livestock production is socioeconomically important and where excessive grazing has occurred, recovery following destocking or even removal of livestock may be minimal. In some cases, it will not even arrest degradation if positive feedbacks have been set in motion.

Despite the broad recognition that discontinuous change is a common feature of many rangelands, little progress has been made towards quantifying transition thresholds for management applications. Management should (a) seek to minimize displacement over critical degradation thresholds; (b) recognize that infrequent, extreme environmental events (e.g., drought) may push systems past critical thresholds and (c) explicitly identify process constraints to recovery following relaxation or removal of stress. A major challenge now facing rangeland ecologists is to identify and characterize ecological processes, plant-soil biota population parameters and soil physical/chemical properties that may provide managers advance warning that a critical transition threshold is being approached. Armed with such information, management could then be adjusted to avert undesirable transitions or to initiate strategic actions to promote desirable transitions. Criteria for classifying landscapes with regard to their transition probability would help prioritize allocation of scarce management resources. Some lands may be past a point of no return; others may be slated to minimize further degradation; still others may be candidates for investing resources to remove constraints to recovery and promote restoration. Reversal of transitions may often require active intervention by land managers. In areas experiencing 'desertification' traditional agronomic approaches to ecosystem restoration are management intensive, costly and seldom successful. Current ecological approaches advocate selective intervention on strategic landscape elements to concentrate scarce resources (water, nutrients, propagules) and establish species capable of initiating autogenic succession and driving progressive rehabilitation (Whisenant et al., 1995; Havstad et al., this volume; Ludwig and Tongway, this volume; Thurow, this volume).

ACKNOWLEDGEMENTS

We thank the organizers of the Rangelands Desertification workshop for the opportunity to participate in this endeavor. The manuscript was improved by helpful comments provided by A. Aradottir. Chad McMurtry assisted with graphics and Veronica Macias helped finalize the references. Their help is much appreciated.

REFERENCES

Aradottir, A., Arnalds, O. and Archer, S. 1992. Degradation of vegetation and soils. In: Icelandic Yearbook of Soil Conservation. Ed. A. Arnalds. pp. 73–82. Soil Conservation Service, Gunnarsholt, Iceland.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? American Nat. 134, 545–561.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. In: Ecological Implications of Livestock Herbivory in the West. Ed. M. Vavra, Laycock, W. and R. Pieper. pp. 13–68. Soc. Range Management, Denver, CO.

Archer, S. 1995. Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2, 83–99.

Archer, S. 1996. Assessing and interpreting grass-woody plant dynamics. In: The Ecology and Management of Grazing Systems. Ed. J. Hodgson and A. Illius. pp. 101–134. CAB International, Wallingford, Oxon, UK.

Archer, S., Scifres, C.J., Bassham, C.R. and Maggio R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecol. Monogr. 58, 111–127.

Archer, S. and Smeins, F.E. 1991. Ecosystem-level processes. In: Grazing Management: An Ecological Perspective. Ed. R. K. Heitschmidt and J. W. Stuth. pp. 109–139. Timberline Press, Portland, OR.

Arnalds, A. 1987. Ecosystem disturbance in Iceland. Arctic Alpine Res. 19, 508–513.

Arnalds, O. 1990. Characterization and erosion of Andisols in Iceland. Ph.D. thesis, Texas A&M University.

Arnalds, O. 1998. Desertification in Iceland. Desertification Control Bulletin 32, 22–24.

Arnalds O. 1999. The Icelandic rofabard soil erosion features. Earth Surface Processes and Landforms. (In press).

Baisan, C.H. and Swetnam, T.W. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Can. J. For. Res. 20, 1559–1569.

Bosch, O.J.H. and Booysen, J. 1992. An integrative approach to rangeland condition and capability assessment. J. Range Manage. 45, 116–122.

Branson, F.A. 1985. Vegetation changes on western rangelands Vol. 2. Soc Range Management, Denver, CO.

Chapin, F.S., III, Bloom, A.J., Field, C.B. and Waring, R.H. 1987. Plant responses to multiple environmental factors. BioScience 37, 49–57.

Chew, R.M. 1982. Changes in herbaceous and suffrutescent perennials in grazed and ungrazed desertified grassland in southeastern Arizona, 1958–1978. Am. Midl. Nat. 108, 159–169.

Clarkson, N.M. and Lee, G.R. 1988. Effects of grazing and severe drought on a native pasture in the Traprock region of southern Queensland. Trop. Grassl. 22, 176–183.

Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. Ecology 68, 1243–1250.

Collins, S.L. and Barber, S.C. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64, 87–94.

Connell, J.H. and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Nat. 111, 1119–1144.

D'Antonio, C.M. and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Ann. Rev. Ecol. Syst. 23, 63–87.

Dublin, H.T., Sinclair, A.R.E. and McGlade, J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. J. Animal Ecol. 49, 1147–1164.

Dyksterhuis, E.J. 1949 Condition and management of rangeland based on quantitative ecology. J. Range Manage. 2, 104–105.

Flinn, R.C., Scifres, C.J. and Archer, S.R. 1992. Variation in basal sprouting in co-occurring shrubs: implications for stand dynamics. J. Vegetation Sci. 3, 125–128.

Foran, B.D. 1986. The impact of rabbits and cattle on an arid calcareous shrubby grassland in central Australia. Vegetatio 66, 49–59.

Friedel, M.H. 1991. Range condition assessment and the concept of thresholds: A viewpoint. J. Range Manage. 44, 422–426.

Fulbright, J.E. and Beasom, S.L. 1987 Long-term effects of mechanical treatment on white-tailed deer browse. Wildlife Soc. Bull. 15, 560–564.

Gadgill, M. and Meher-Homji, V.M. 1985. Land use and productive potential of Indian savannas. In: Ecology and Management of the World's Savannas. Eds. J.C. Tothill and J.J. Mott. pp. 107–113. Australian Academy of Science, Canberra.

George, M.R., Brown, J. R. and Clawson, W. J. 1992. Application of non-equilibrium ecology to management of Mediterranean grasslands. J. Range Manage. 45, 436–440.

Godran, M. and Forman, R.T.T. 1983. Landscape modification and changing ecological characteristics. In: Disturbance and Ecosystems. Eds. H.A. Mooney and M. Godron. pp. 12–28. Ecological Studies 44. Springer-Verlag, New York.

Herbel, C.H., Ares, F.N. and Wright, R.A. 1972. Drought effects on a semi-desert grassland. Ecology 53, 1084–1093.

Hibbard, K.A. 1995. Landscape patterns of carbon and nitrogen dynamics in a subtropical savanna: observations and models. Ph.D. dissertation, Texas A&M Univ., College Station.

Hobbie, S.E. 1992 . Effects of plant species on nutrient cycling. Trends Ecol. Evol. 7, 336–339.

Hobbs, R.J. 1994. Dynamics of vegetation mosaics: Can we predict responses to global change? Ecoscience 1, 346–356.

Jones, R.M. 1992. Resting from grazing to reverse changes in sown pasture composition: application of the 'state-and-transition' model. Trop. Grassl. 26, 97–99.

Joyce, L.A. 1993. The life cycle of the range condition concept. J. Range Manage. 46, 132–138.

Kieft, T.L., White, C.S., Loftin, S.R., Aguilar, R., Craig J.A. und Skaar D.A. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. Ecology 79, 671–683.

Laycock, W.A. 1991 Stable states and thresholds of range condition on North American rangelands: A viewpoint. J. Range Manage. 44, 427–433.

Lockwood, J.A. and Lockwood, D.R. 1993 Catastrophe theory – a unified paradigm for rangeland ecosystem dynamics. J. Range Manage. 46, 282–288.

Loucks, O.L., Plumb-Mentjes, M.L. and Rogers, D. 1985. Gap processes and large-scale disturbances in sand prairies. In: The Ecology of Natural Disturbance and Patch Dynamics. Eds. S.T.A. Picket and P.S. White. pp. 71–83. Academic Press, Inc., New York.

Luken, J. 1990. Directing Ecological Succession. Chapman and Hall, London.

Mack, R.N. 1981. Invasion of Bromus tectorum L. into western North America, and ecological chronicle. Agroecosystems 7, 145–165.

McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol. Monogr. 53, 291–320.

Milton, S.J. 1992. Effects of rainfall, competition and grazing on flowering of Osteospermum sinuatum (Asteraceae) in arid Karoo rangeland. J. Grassland Soc. South Africa 9, 158–164.

Milton, S.J. and Hoffman, M.T. 1994 The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. African J. Range Science 11, 18–26.

National Research Council 1994. Rangeland health: new methods to classify, inventory and monitor rangelands National Academy Press, Washington, DC.

Neilson, R.P. 1986 High-resolution climatic analysis and Southwest biogeography. Science 232, 27–34.

O'Connor, T.G. 1993. The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. J. Appl. Ecol. 30, 119–132.

O'Connor, T.G. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. J. Appl. Ecol. 31, 155–171.

Orr, D.M., Evenson, C.J., Lehane, J.K., Bowly, P.S. and Cowan, D.C. 1993. Dynamic of perennial grasses with sheep grazing in Acacia aneura woodlands in south-west Queensland. Trop. Grassl. 27, 87–93.

Overpeck, T., Rind, D. and Goldberg, R. 1990. Climate-induced changes in forest disturbance and vegetation. Nature 343, 51–53.

Rapport, D.J. and Whitford, W.G. 1999. How ecosystems respond to stress. BioScience 49, 193–203.

Reid, N., Marroquin, J., Beyer-Münzel, P. 1990. Utilization of shrubs and trees for browse, fuelwood and timber in Tamaulipan thornscrub, northeastern Mexico. Forest Ecol. Manage. 36, 61–79.

Rykiel, E.J. Jr. 1985. Towards a definition of ecological disturbance. Australian J. Ecology 10, 361–365.

Savage, M. and Swetnam, T.W. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. Ecology 71, 2374–2378.

Schlatterer, E.F. 1989. Toward a user-friendly ecosystem: myth or mirth? In: Proceedings, Land Classifications, Based on Vegetation: Applications for Resource Management. Eds. D.E. Ferguson, P. Morgan and F.D. Johnson. pp. 223–227. General Technical Report INT-257. USDA Forest Service, Intermountain Research Station, Ogden, Utah.

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.

Scholes, R. and Archer, S. 1997. Tree-grass interactions in savannas. Ann. Rev. Ecol. Syst. 28, 517–544.

Scifres, C.J., Hamilton, W.T., Inglis, J.M. and Conner, J.R. 1983. Development of integrated brush management systems (IBMS): decision-making processes. In: Proceedings Brush Management Symposium. Ed. K.W. McDaniel. pp. 97–104. Texas Tech Press, Lubbock.

Smeins, F.E. and Merrill, L.B. 1988. Long-term change in semi-arid grassland. In: Edwards Plateau Vegetation. Eds. B.B. Amos and F.R. Gehlback. pp. 101–114. Baylor Univ. Press, Waco, TX.

Stokes, C.J. 1994 Degradation and Dynamics of Succulent Karoo Vegetation. Published, Place University of Natal, Pietermaritzburg, South Africa.

Swetnam, T.W. and Betancourt, J.L. 1990. Fire-southern oscillation relations in the southwestern United States. Science 249, 1010–1020.

Verstraete, M.M. 1986. Defining desertification: a review. Climatic Change 9, 5–18.

Watson, I.W., Burnside, D.G. and Holm, A.M. 1996. Event-driven or continuous: which is the better model for managers? The Rangeland J. 18, 351–369.

Watson, I.W., Westoby, M. and Holm A.M. 1997a. Continuous and episodic components of demographic change in arid zone shrubs: models of two Eremophila species from western Australia compared with published data on other species. J. Ecology 85, 833–846.

Watson, I.W., Westoby, M. and Holm, A.M. 1997b. Demography of two shrub species from an arid grazed ecosystem in Western Australia 1983–93. J. Ecology 85,815–832.

West, N. E. 1986. Desertification or xerification? Nature 321, 562–563.

Westoby, M., Walker, B. and Noy-Meir, I. 1989a. Opportunistic management for rangelands not at equilibrium. J. Range Manage. 42, 266–274.

Westoby, M., Walker, B. and Noy-Meir, I. 1989b. Range management on the basis of a model which does not seek to establish equilibrium. J. Arid Environ. 17, 235–239.

Whisenant, S.G., Thurow, T.T. and Maranz, S.J. 1995. Initiating autogenic restoration on shallow semiarid sites. Restoration Ecology 3, 61–67.

Whitford, W.G., Martinez-Turanzas, G. and Martinez-Meza, E. 1995. Persistence of desertified ecosystems: explanations and implications. In: Desertification in Developed Countries. Eds. D.A. Mouat and C.F. Hutchinson. pp. 319–332. Kluwer Academic Publishers. London.

Yassoglou, N.J. and Kosmas, C. 1999. Desertification in the Mediterranean Europe. In: Rangeland Desertification, International Workshop, Iceland, September 1997. Eds. O. Arnalds and S. Archer. RALA Report no. 200. (In press).