REGULATION OF ECOSYSTEM STRUCTURE AND FUNCTION: CLIMATIC VERSUS NON-CLIMATIC FACTORS

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24.1 INTRODUCTION

Ecological studies seek to ascertain how interactions between organisms (e.g., competition, predation, herbivory), interactions between organisms and their environment (e.g., atmosphere, soils, climate), and perturbation or disturbances such as fire, flooding and high wind might explain and predict variations in the distribution and abundance of plants and animals and the structure and function of ecosystems. Among the myriad possible interactions between biotic (living) and abiotic (nonliving) components of ecosystems, it is desirable to identify the combinations that constitute primary, secondary, and tertiary controls over patterns and processes.

Regional physiognomy (i.e., gross vegetation structure: forest, grassland, or shrubland) may largely reflect the prevailing macroclimate (Box, 1981). However, substantial variation occurs across landscapes within a region, and broadscale climatic variables cannot account for the spatial patterns that shape local ecosystem characteristics. As spatial and temporal frames of observation are diminished and resolution is increased, edaphic heterogeneity and disturbances (such as grazing, fire, cropping, and flooding) assume greater importance in determining ecosystem structure and function. Seasonal and annual variability in weather will dictate the productivity and dynamics of populations over time. Soils, topography, and elevation will influence patterns of plant distribution, growth, and abundance over the landscape, and these localized variations in plant distribution will subsequently influence animal distribution and abundance.

The utilization of plants by animals (grazers, browsers, granivores) will be superimposed on this background of topo-edaphic heterogeneity and climatic variability to further influence ecosystem structure and function. As a result, plant species whose adaptations to the prevailing climate and soils would make them the competitive dominants of the community when herbivore populations are low may assume subordinate roles or even face local extinction when certain herbivores are present. Understanding ecosystem structure and function thus requires a working knowledge of the degree of interaction between plant, animal, and environmental components across an array of spatial and temporal scales.

Over the geologic past, conditions in the atmosphere, oceans, and biosphere have followed natural cycles. However, in recent history, human activities have become an increasingly important force driving changes in the environment. Scientific theory and evidence indicate that the extraction and utilization of resources by rapidly expanding human populations have the potential to induce profound changes in the global environment. Intensification of industrial and land-use practices have increased concentrations of greenhouse gases and have altered surface energy flux and biophysical features in ways that could produce shifts in climate and thus affect ecosystem processes. On the other hand, the impact of gradual shifts in climatic features on ecosystems may be distant and minor in relation to more immediate impacts associated with pollution, deforestation, cropping, livestock grazing, and other consumptive uses of resources. It is thus becoming increasingly important to distinguish the role of climatic factors relative to non-climatic factors in shaping ecosystems.
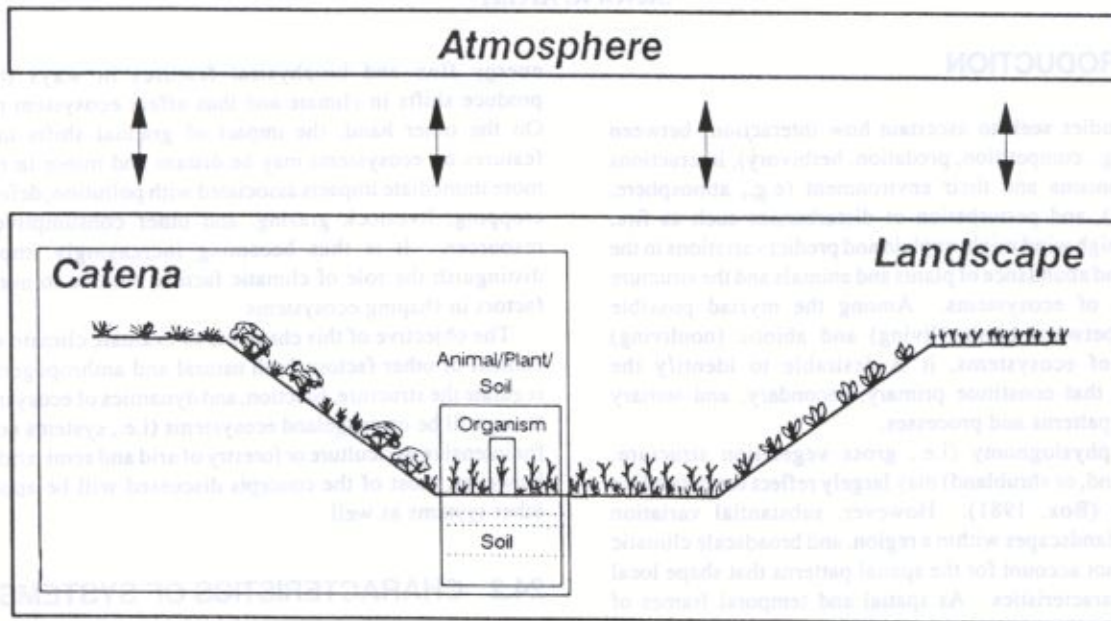
The objective of this chapter is to evaluate climate within the context of other factors, both natural and anthropogenic, which regulate the structure, function, and dynamics of ecosystems. The focus will be on rangeland ecosystems (i.e., systems not utilized for intensive agriculture or forestry of arid and semi-arid regions.) However, most of the concepts discussed will be applicable in other systems as well.

24.2 CHARACTERISTICS OF SYSTEMS

Ecosystems are dynamic, complex, and difficult to define or delimit in space and time. How do we go about making sense of all this complexity so as to meaningfully evaluate the relationships between organisms with each other and their environment? Hierarchical ordering has been applied to multilevel ecological systems to provide a conceptual framework for practical definition. Systems, including ecological systems, are groups of interacting, interdependent parts operating together for some purpose. In ecosystems, the flow of energy and the cycling of nutrients is the result of organisms interacting with each other and their environment. Systems have unique characteristics or emergent (nonreducible) properties which are manifest only when components interact to produce larger functional wholes– hence, the axioms "the whole is greater than the sum of the parts" and "a forest is more than just a collection of trees." A system's principal attribute is that we can understand it fully only if we view it as a whole. Water, for example, might be considered a system composed of hydrogen and oxygen components. However, the physical and chemical attributes of hydrogen and oxygen by themselves could not be used to predict the unique physical characteristics of H_2O. In ecological systems, the study of individual organisms does not reveal the unique properties of higher levels of organization that emerge from interactions of organisms with each other and their environment.

Because ecological systems are complex and are composed of many interacting parts, it is useful to view their organization as a hierarchy, or a graded series with several levels of organization– for example, organisms, populations, communities, ecosystems, and landscapes (Rowe, 1961, MacMahon et al., 1978, Allen and Starr, 1982). Any level of organization in the hierarchy can be

Figure 24.1. Conceptual integration of climatological, biological and pedological hierarchies (from Archer and Smeins, 1991; reprinted by permission of Timber Press).

Atmosphere

Catena

Landscape

Animal/Plant/Soil

Organism

Soil

LEVEL/ PROCESSES	TIME SCALE	SPATIAL SCALE
SOIL		
Weathering		
Illuviation/elluviation	decades/ centuries	m^2
Pedogenesis		
ORGANISM		
Acquisition/allocation of resources	hours, days	m^2
Metabolism		
ANIMAL/PLANT/SOIL		
Mineralization		
Mass Flow/Diffusion		
Chemical Equilibria		
Wet/Dry Deposition	months/ years	m^2 to ha
Competition		
Grazing		
Evapotranspiration		
Population Dynamics		
Succession		

LEVEL/ PROCESSES	TIME SCALE	SPATIAL SCALE
CATENA		
Short-Range Transport:	years/ decades	ha
- Runoff/Runon		
- Erosion		
- Interflow		
- Grazing Animals		
LANDSCAPE		
Long-Range Transport:	decades/ centuries	km^2
- Stream Discharge		
- Local Atmospheric Circulation		
- Export of Plant/Animal Matter		

represented as a system, and interactions with the physical environment at each level produce a characteristic, functional system. The components of ecosystems (plants, animals, microbes, geologic substrates, soils, climate) interact and are dependent upon one another for the flow of energy and cycling of nutrients. Each level of organization has characteristic processes that operate at prescribed spatial and temporal scales (Woodmansee and Adamsen; 1983, Woodmansee, 1988).

In the conceptual ecological hierarchy in Fig. 24.1, each level of organization is characterized by key processes, inputs, and outputs. Energy and matter are exchanged between components within a level and between levels. In this scheme, an "ecosystem" would simply be a biotic community (plants, microbes, herbivores, carnivores) in association with a given soil body. A "catena" is comprised of linked ecosystems. The landscape is a hierarchical level composed of catenas, and landscapes form regional land systems, etc. Climate constitutes a backdrop against which ecosystem processes operate at various spatial and temporal scales.

In contrast to reductionism, hierarchy theory permits evaluation of a complex system without reducing it to a series of simple, disconnected subsystems. No single level in the hierarchy of an ecological system should be considered fundamental. Understanding a system at one level of organization requires knowledge of the levels both above and below the targeted level (Webster, 1979, Allen et al., 1984). Interpreting the behavior of a system at one level of organization without consideration of adjacent levels may generate misleading results. Studies at the individual plant level often do not take into account key processes operating at the community level of organization. Thus, studies in a controlled environment on the effects of seasonal availability of moisture on plant growth may not enable one to predict the response of that plant in a community setting, where species with other adaptations are competing for moisture while simultaneously integrating constraints imposed by nutrient availability, herbivory, temperature and light.

Species comprising a community of plants possess different adaptations. As a result, the growth of each species may be
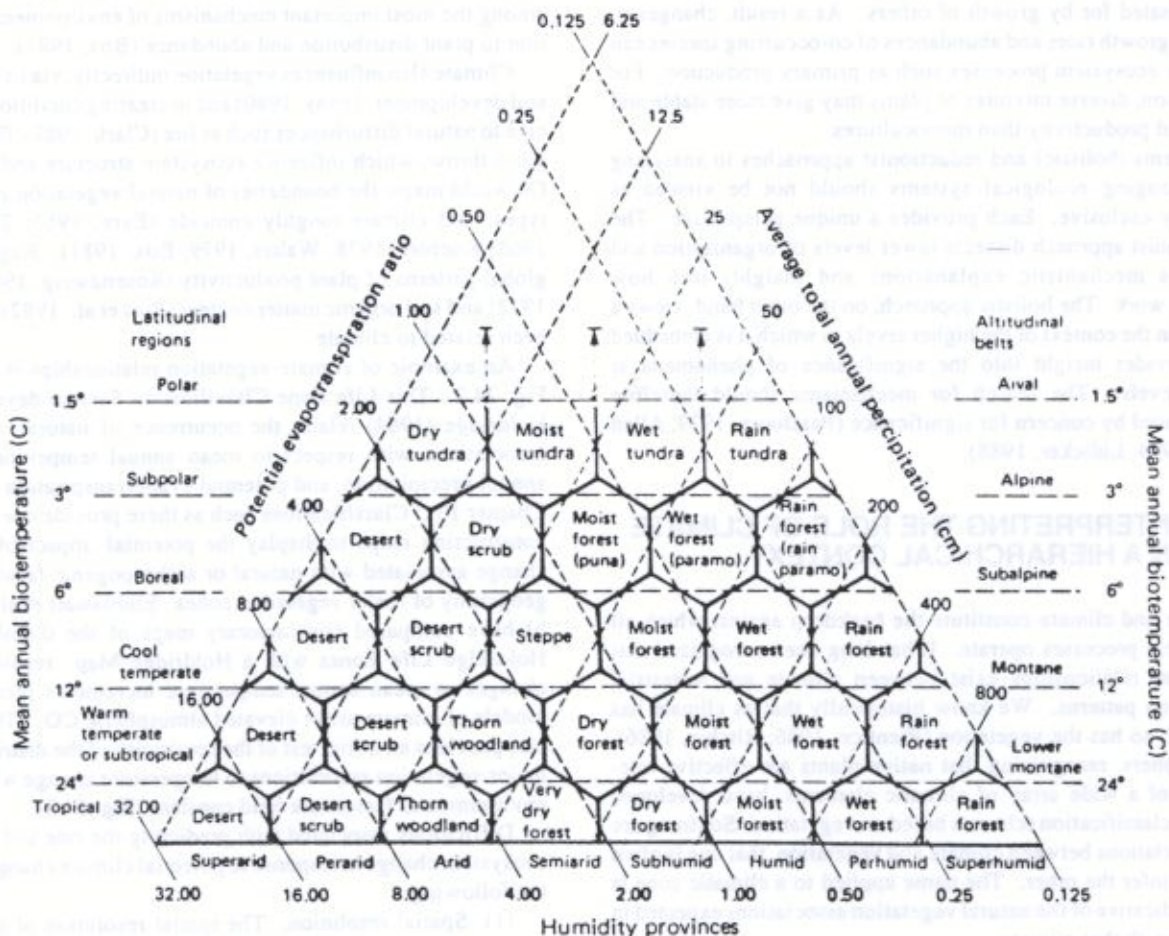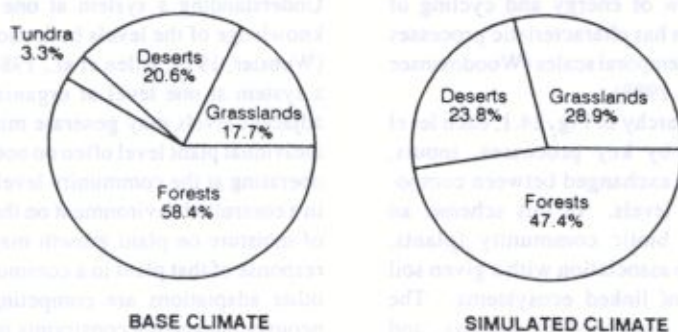

Figure 24.2. Holdridge Life Zone System for classifying plant formations (after Holdridge, 1964; reprinted by permission of AAAS).

Figure 24.3. Projected changes in areal extent of biomes resulting from changes in mean annual temperature increments predicted by models of climate under elevated atmospheric CO_2 (from Emanuel, et al., 1985a; reprinted by permission of Kluwer Academic Publishers).

BASE CLIMATE

Tundra 3.3%
Deserts 20.6%
Grasslands 17.7%
Forests 58.4%

SIMULATED CLIMATE

Deserts 23.8%
Grasslands 28.9%
Forests 47.4%

limited by a different combination of environmental factors. Fluctuations in weather cause production of individual species to vary substantially from year to year. However, production of the whole community is more stable, because years favorable for growth of some species cause a compensatory decrease in growth of other species (Chapin and Shaver 1985). Conversely, in stressful years, the loss of productivity of some species is compensated for by growth of others. As a result, changes in relative growth rates and abundances of co-occurring species can stabilize ecosystem processes such as primary production. For this reason, diverse mixtures of plants may give more stable and sustained productivity than monocultures.

Systems (holistic) and reductionist approaches to analyzing and managing ecological systems should not be viewed as mutually exclusive. Each provides a unique perspective. The reductionist approach dissects lower levels of organization and provides mechanistic explanations and insights into how systems work. The holistic approach, on the other hand, views a system in the context of the higher levels in which it is embedded and provides insight into the significance of phenomena at lower levels. The search for mechanisms should therefore be balanced by concern for significance (Passioura, 1979, Allen et al.; 1984, Lidicker, 1988).

24.3 INTERPRETING THE ROLE OF CLIMATE IN A HIERARCHICAL CONTEXT

Weather and climate constitute the backdrop against which all ecosystem processes operate. It has long been recognized that important relationships exist between climate and terrestrial vegetation patterns. We know historically that as climate has changed, so has the vegetation (Prentice, 1986; Ritchie, 1986). Geographers, recognizing that native plants are effective integrators of a wide array of climatic elements, have developed climate classification schemes based on vegetation. So strong are the correlations between climate and vegetation, that one is often used to infer the other. The name applied to a climatic zone is often indicative of the natural vegetation associations expected in regions with that climate.

Climate exerts both direct and indirect influences on the vegetation. General levels and seasonal patterns of solar radiation, temperature, precipitation, and soil moisture have a direct

bearing on the growth and survival of land plants. Plants, in turn, have adapted to varying climatic conditions through modification of form and foliar structures, physiological processes, and seasonal habits, and their presence on the land subsequently modifies soils and microclimate. Climatic limits to the adequacy of particular combinations of leaf and plant size, shape, and longevity, as measured by positive water and energy balances, are among the most important mechanisms of environmental limitation to plant distribution and abundance (Box, 1981).

Climate also influences vegetation indirectly, via its effects on soil development (Jenny, 1980) and in creating conditions conducive to natural disturbances such as fire (Clark, 1988), floods, and wind-throw, which influence ecosystem structure and function. On world maps, the boundaries of natural vegetation zones, soil types, and climate roughly coincide (Eyre, 1963; Trewartha, 1968; Kuchler, 1978; Walter, 1979; Box, 1981). Regional and global patterns of plant productivity (Rosenzweig, 1968, Lieth, 1972) and soil organic matter content (Post et al., 1982) have also been related to climate.

An example of climate-vegetation relationships is shown in Fig. 24.2. This Life Zone Classification System developed by Holdridge (1964) relates the occurrence of natural vegetation associations with respect to mean annual temperature, mean annual precipitation, and potential evapotranspiration (See also Chapter 13). Classifications such as these provide one means of constructing maps to display the potential impact of climatic change associated with natural or anthropogenic factors on the geography of major vegetation zones. Emmanuel et al. (1985 a, b) have compared contemporary maps of the distribution of Holdridge Life Zones with a Holdridge Map resulting from changes in mean annual temperature increments predicted by models of climate under elevated atmospheric CO_2. Their exercise provides an initial test of the sensitivity of the distribution of major vegetation associations to temperature change when other environmental factors are held constant (Fig. 24.3).

Difficulties associated with predicting the rate and extent of ecosystem change in response to potential climate change include the following:

(1) Spatial resolution. The spatial resolution of predictive climate models is substantially coarser than the resolution of regional vegetation maps. Climate simulation models typically integrate over much greater spatial scales (e.g., kilometers) than

do most ecosystem simulation models (e.g, meters). In addition, climates of particular places may change in ways not predictable from large-scale changes (Wigley, et al., 1985).

(2) Aspects of climate important to vegetation may not be adequately simulated by climate models. These include:

a. Compensating or reinforcing interactions among temperature, humidity, radiation, and rainfall.

b. Changes in the spatial and temporal (seasonal) variability of key parameters such as rainfall.

c. Changes in the frequency, magnitude, and timing of extreme events (such as drought or floods, high or low temperatures, high winds). Rare or infrequent (episodic) events may do more to shape ecosystem attributes than changes in mean climatic variables. Infrequent but extreme climatic events may be especially important in masking or confounding patterns of vegetation change (Beatley, 1974; MacMahon, 1980; Chew, 1982; Griffin and Friedel, 1985; Turner, 1990).

(3) The effects of climate may act in subtle or obscure ways to influence ecosystems. As a result, changes in ecosystem structure related to climate may be mistakenly attributed to other factors. Western and Van Praet (1973) document a case of regional mortality of *Acacia zanthophlœa* (fever tree) woodlands in the Amboseli Basin of East Africa. The decline of the woodlands was accompanied by a marked shift toward a more arid (e.g., desertified) habitat, with excessive grazing by pastoralist livestock commonly regarded as the principle cause. However, subsequent research demonstrated that livestock grazing was concentrated around the perimeter of the basin where tree mortality was low. Toward the interior of the basin where tree mortality approached 100 percent, livestock were absent. Additional data indicated fever trees to be highly intolerant of salts and that tree stands in an advanced stage of decline were associated with saline soils. Western and Van Praet present evidence that these woodlands had developed over a period of decades when the water table was low; later, during a series of high rainfall years, the water table rose three to four meters and introduced high levels of salts into the tree rooting zones causing their demise. Thus, long-term, climate-induced oscillation in the water table, not livestock grazing, was the proximate driving force for vegetation change.

(4) Relatively small changes in climate that might have a negligible influence within life zones could cause substantial changes in transitional areas. Organisms near the extremes of their range are typically most sensitive to change. Natural life-form ecotones (transition zones) cover about 30 percent of the earth's land area (Box, 1981), and slight shifts in climate may have a greater impact on vegetation in these areas than might otherwise be predicted.

(5) Topography, elevation and other edaphic factors may constrain vegetation response to climate. Many soil properties are closely correlated with climate (Jenny, 1980) and are therefore reflected in climate-vegetation classification schemes. However, physical and geological features such as parent material, texture, and slope aspect and inclination are not taken into account in climatic treatments. Figure 24.4 illustrates how vegetation structure may range from a grassland with scattered woody plants to a woodland with scattered grasses over a wide range of annual rainfall (800-1200 mm), depending on soil texture. In addition, the present soils may largely reflect characteristics developed over the past centuries, and their ability to support an alternate vegetation that might otherwise be well-adapted to future climatic regimes may be limited. Changes in soil properties would lag far behind changes in climate and would be constrained by parent material and geomorphology.

(6) The dynamics of ecosystems and their attributes are significantly influenced by disturbance. Disturbance and perturbation interact with climatic variability to influence ecosystem dynamics at various spatial and temporal scales. On a large scale, precipitation and temperature regulate vegetation dynamics in arid and semi-arid systems (MacMahon, 1980; Austin et al., 1981; Sala, et al., 1988). However, most plant communities and landscapes are extremely patchy (Belsky, 1983) and broad-scale climatic factors cannot account for the existence of these small-scale patterns. Frequent, small-scale perturbations such as ant, termite, or rodent mounds or patchy grazing occur within the context of larger-scale, less frequent disturbances such as fires, floods, and windstorms, to produce complex disturbance regimes (Collins, 1987) which shape ecosystem structure and function. Interpreting community composition and productivity is, thus, contingent upon our ability to understand the interactive role of concurrent, multiple-scale disturbances (Loucks et al.; 1985, Collins and Barber, 1985; Collins, 1987).

The type of disturbance (e.g., grazing, fire, flooding) and its frequency and intensity operate against a backdrop of climatic variability to influence ecosystem structure. Thus, in locations where the climate and soils might support forest or woodland, periodic fire or the preferential consumption of woody plant foliage or seeds by animals and insects can maintain a grassland or savanna (Belsky, 1984; Berdowski, 1987; Naiman, 1988; Yeaton, 1988). Conversely, the preferential utilization of grasses by domestic livestock or native herbivores and granivores can cause shrub- and woodlands to develop in areas that might otherwise be grasslands (Brown and Heske, 1990; Archer and Smeins, 1991). Unfortunately, annual estimates of the numbers or biomass of animals in ecosystems and the importance of fauna in regulating plant productivity and composition are seldom available. As a result, it is difficult to gauge their importance. Changes in vegetation that might be expected to accompany changes in climate may therefore not be realized unless biotic factors dictating ecosystems properties are simultaneously altered.

In many parts of the world, anthropogenic activities are thought to have caused widespread changes in vegetation and even desertification. However, it is often difficult to assess the extent to
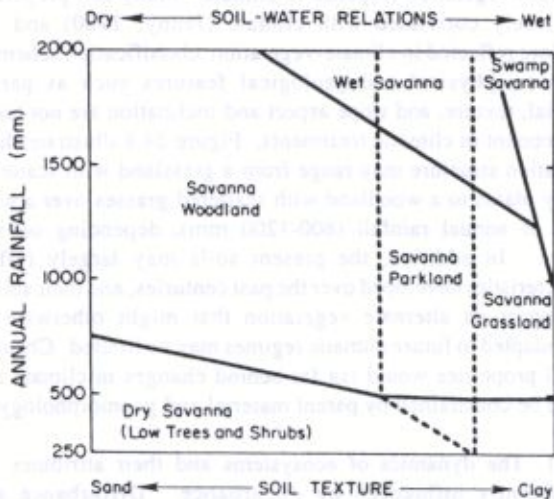
Figure 24.4. Classification of savannas of the world based on annual rainfall and soil texture (from Johnson and Tothill, 1985). Note the role of a local factor (soil texture) in regulating vegetation structure within the context of a long-term, regional climatic factor (annual rainfall). (Reprinted by permission of the Australian Academy of Science).

which disturbances have influenced ecosystems relative to climatic factors which may be operating simultaneously (Herbal et al., 1972; McNaughton, 1983; Foran, 1986). Figure 24.5 shows a case where the influence of grazing on vegetation was minor relative to the changes caused by variations in rainfall. Retrogression or desertification can be natural (Haynes, 1982), man-induced (Owen, 1979; Gornitz and NASA, 1985), or a combination of the two (Hastings and Turner, 1965, Verstraete, 1986). Human activities likely magnify or accelerate changes that might otherwise be caused by climate alone. Retrogression associated with disturbance may be mitigated when climatic conditions are favorable or magnified in unfavorable years. Succession or recovery following disturbance can be accelerated under favorable climatic conditions or arrested under unfavorable conditions.

(7) It is difficult to distinguish between directional change and fluctuation. Changes in ecosystem status over time may represent fluctuation, retrogression, or succession (Fig. 24.6). Fluctuation represents reversible changes in dominance within a stable species composition, whereas succession and retrogression are directional changes in composition and dominance (Rabotnov, 1974). Chronic disturbance or changes in environmental conditions can cause retrogression (desertification), which eventually leads to a loss of diversity, net primary production, and ground cover. During the course of retrogression, site processes become increasingly coupled to and regulated by abiotic factors. This, in turn, may accentuate fluctuation. Progressive directional changes, termed succession, occur in the opposite direction and represent the recovery of ecosystem structure following biotic or abiotic disturbance. As plant diversity, production, and ground cover increase through time, the plants themselves exert substantial control over microclimate, energy flow, nutrient cycling, and species interactions, thus dampening fluctuation associated with

oscillation of weather and abiotic factors.

While the concepts of directional change versus fluctuation are rather straightforward, climate and vegetation data bases typically do not cover long enough time periods to enable these critical distinctions to be made. Had the data in Fig. 24.5 been collected only between 1932 and 1940 (a long-term study by all standards!), retrogression would have been documented. Had the study been conducted between 1936 and 1943, it would have been concluded that successional changes were occurring. However, when the data are viewed in their entirety, we see that fluctuation, not directional change, has occurred.

Even when fairly detailed long-term records are available, our understanding of what causes some sites to fluctuate while others change in a directional fashion may be limited. Collins et al. (1987) analyzed 39 years of vegetation data from two Oklahoma sites grazed by cattle. Each site contained an exclosure to prevent cattle from grazing portions of each pasture. The vegetation in the grazed areas of both pastures exhibited shifting patterns of abundance rather than sequential species replacement (i.e., fluctuation), as did one of the exclosures. The other exclosure exhibited a directional change from dominance by annuals to dominance by perennial grasses. Reasons for the contrasting behaviors were not clear.

(8) Ecosystems have inertia. The extent to which shifts in vegetation structure lag behind the climatic changes that drive them and the extent to which vegetation can ever be said to be in equilibrium with climate are not easily identified (Davis, 1982). For example, vegetation which established from seed under a previous climatic regime may survive under the present regime in a vegetative state. This phenomenon, whereby plants persist for periods of tens to hundreds of years under conditions very different from those under which they initially became established, is
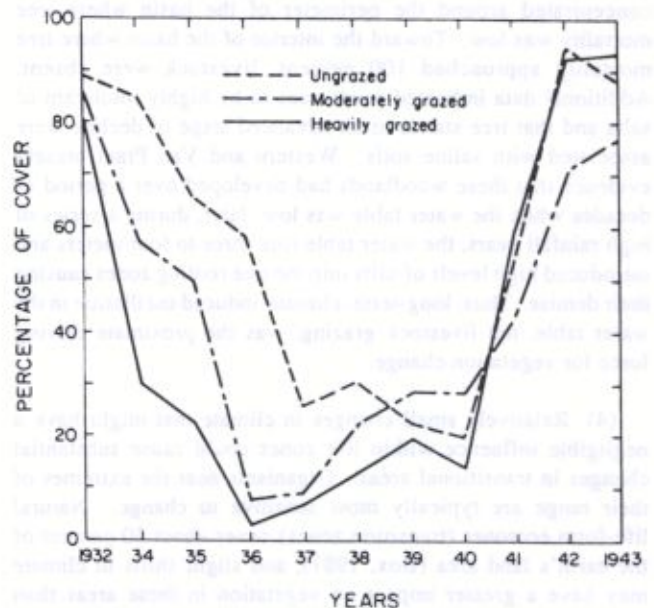

Figure 24.5. Changes in percentage basal cover in the shortgrass steppe vegetation type during and after drought (from Weaver and Albertson (1944, 1956) as shown in Branson (1985).
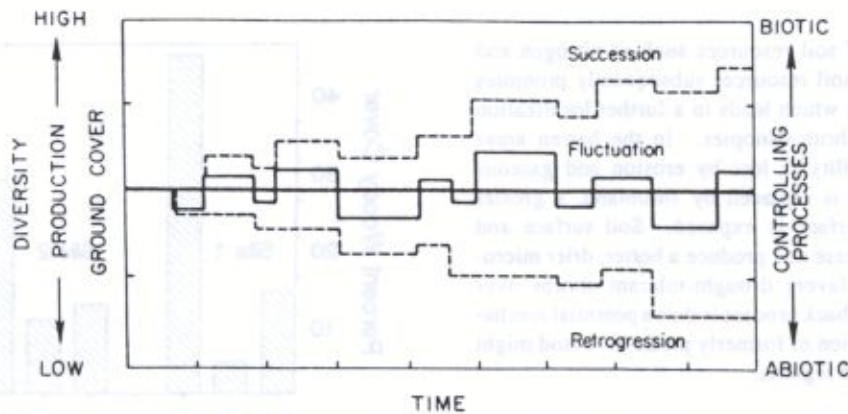
Figure 24.6. Hypothetical changes in species composition over a number of climatic cycles (from Archer and Smeins, 1991). All lines illustrate the role of climatic variability in causing community composition to fluctuate through time. The upward path represents succession, whereas the downward path represents retrogression. (Reprinted by permission of Timber Press).

known as biological inertia (Cole, 1985, Lewin, 1985). If climatic conditions today are such that the dominant plants cannot successfully reestablish from seed with sufficient frequency to maintain the population, community composition is destined to change. Correlations between recent changes in vegetation and climatic variables or disturbance regimes may be thus spurious or low. The apparent displacement of grasses by shrubs in the deserts of southwestern North America over the past 100 years may exemplify this phenomenon (Neilson, 1986).

(9) Changes in ecosystem structure can be abrupt and non-linear. As Fig. 24.6 implies, changes in ecosystem configurations may be stepwise rather than linear. Thus, an assemblage of plants may be rather stable and resistant to disturbance or climate change up to certain thresholds. Beyond these threshold levels, changes can be rapid, dramatic, and potentially irreversible over reasonable time frames (Griffin and Friedel, 1985; Johnstone, 1986, Archer, 1990). Climate or disturbance may generate episodes of plant establishment or mortality whose impacts on ecosystem structure are maintained long after the triggering event has passed.

24.4 EVALUATING PROXIMATE CAUSES OF ECOSYSTEM CHANGE

The preceding section highlights some of the problems and pitfalls in identifying and evaluating causes of ecosystem change. Three concepts of importance in evaluating the cause of change in ecosystems are (1) interactions; (2) necessary and sufficient conditions; and (3) feedbacks.

24.4.1 INTERACTIONS

In statistical experiments, the significance of main effects and interactions are tested. In an ecosystem context, we are interested in identifying the primary factors governing ecosystem processes (i.e. the main effects) and the extent to which the influence of those primary factors might be mediated (lessened or magnified)

when other factors are operational (i.e. their interactions). Main effects in ecosystems could include things such as climate, soils, fire, and grazing. Unfortunately, because of logistical constraints, most ecological studies can focus on but one of these main effects. Results from such studies are thus somewhat out of context, since other potentially important factors and interaction terms are not taken into account. Simulation models are one tool for circumventing this problem. However, the degree to which such models can successfully represent a system will be directly related to our level of understanding and the quality and availability of information used in their construction.

24.4.2 NECESSARY AND SUFFICIENT CONDITIONS

It is necessary for some conditions to change if ecosystems are to change. However, because of thresholds and inertia, a change in some conditions does not necessarily mean that a change in ecosystem status will occur. Thus, certain kinds of changes may be necessary but by themselves not sufficient to elicit a change in ecological systems. The influence of changing a certain variable(s) on ecosystem structure will be determined by the magnitude, direction, and duration of change and the extent to which the change is either augmented or negated by other variables.

24.4.3 FEEDBACKS

Interactions among ecosystem components are often regulated by positive or negative feedbacks which confer a degree of homeostasis. Positive feedbacks are those which reinforce deviations from a set point, whereas negative feedbacks are those which halt or reverse movement away from a steady-state condition. Positive feedbacks can thus accelerate change, whereas negative feedbacks may enable systems to resist change. Schlesinger et al. (1990) hypothesize that positive feedbacks are operational in desertification. In their scenario, long-term grazing of semi-arid grasslands by livestock produces spatial and

temporal heterogeneity of soil resources such as nitrogen and water. Heterogeneity of soil resources subsequently promotes invasion by desert shrubs, which leads to a further localization of soil resources under shrub canopies. In the barren areas between shrubs, soil fertility is lost by erosion and gaseous emissions. As grassland is replaced by shrubland, a greater percentage of the soil surface is exposed. Soil surface and air temperatures thus increase and produce a hotter, drier micro- and mesoclimate which favors drought-tolerant shrubs over grasses. This positive feedback process is thus a potential mechanism by which desertification of formerly productive land might occur in arid and semi-arid regions.

24.4.4 EXAMPLES FROM CASE STUDIES

Numerous studies in North America indicate the replacement of grasslands and savannas by shrublands and woodlands since settlement (Chew and Chew, 1965; Blackburn and Tueller, 1970; Young and Evans, 1981; McPherson, et al. 1988; Archer, 1989). In many instances, these changes in vegetation structure are regarded as undesirable because they have reduced the carrying capacity of the land for livestock or have contributed to retrogression (Fig. 24.6). Similar changes in gross vegetation structure have been reported for Africa (Barnes, 1979; Wickens and Whyte, 1979; van Vegten, 1983), India (Singh and Joshi, 1979), Australia (Walker and Gillison, 1982), and South America (Schofield and Bucher, 1986).

That these plant growth-form transformations have occurred over similar time frames and over such broad geographic areas constitutes one line of evidence that broad-scale factors like climate change may be operating. Local and regional studies also offer some evidence that seasonal patterns of rainfall and temperature may have changed in recent history to favor woody plants over grasses in portions of North America (Hastings and
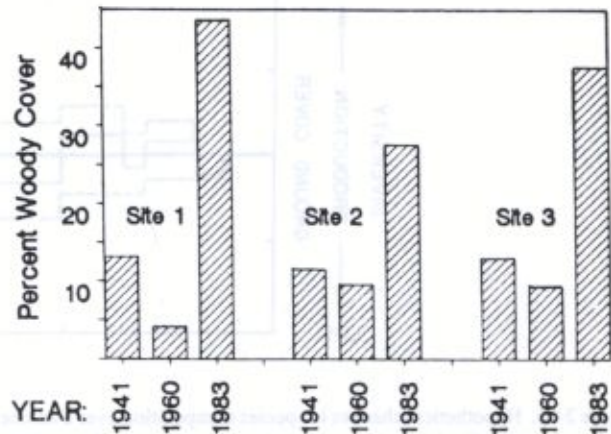

Figure 24.7. Changes in woody plant cover on three sites in a southern Texas savanna parkland between 1941 and 1983 (from Archer, et al., 1988). The 1941-1960 period included a major drought in the 1950s. Annual rainfall during the 1960-1983 period was normal to above-normal. The sites were free of fire and cattle grazing was heavy and continuous through most of the 42-year period. (Reprinted by permission of the Ecological Society of America).

Turner, 1965; Neilson, 1986). Grasslands and savannas which established under previous climatic regimes may have been only marginally supported by the recent climate and were perhaps prone to woody plant invasion (Neilson, 1986, 1987). In addition, oscillations between different climatic regimes in recent history (Mitchell, 1980) may have caused shifts in plant recruitment patterns to promote episodes of woody plant seed production and seedling establishment, but not necessarily their local extinction (Neilson and Wullstein, 1985). However, changes or fluctuations in broad-scale climatic regimes cannot explain how grasslands and savannas have persisted on some sites within a climatic zone

Figure 24.8. Fenceline contrast in the Mitchell grasslands of Queensland, Australia. The fact that variables related to soils and climate would have been similar on both sites suggests factors other than these are controlling vegetation structure on a local scale. (Photo: S. Archer).
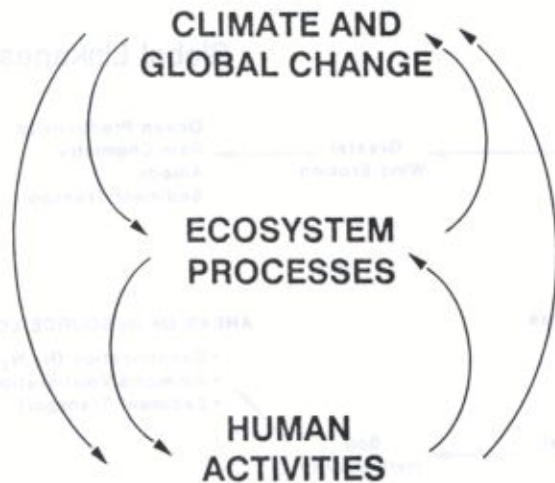
Figure 24.9. Conceptual linkages and feedbacks between climate, ecosystem processes and human activities (Archer, unpublished). See Fig. 24.10 for a more detailed example.

but not others. These changes in vegetation structure around the world have also been coincident with the introduction of domestic livestock and the intensification of grazing pressure.

On a local scale, fire, grazing, and soil properties interact within a variable climate to determine the balance between grasses and woody plants. Figure 24.7 illustrates how woody plant abundance has increased over a 42-year period in savannas of southern Texas. In this system, changes in woody plant abundance have been punctuated and abrupt and not gradual or linear. However, because of the interaction of numerous factors, we can only speculate about causes for the observed change. This site had been heavily grazed by livestock since the early 1900s and fire free. The period between 1941 and 1960 was characterized by severe drought in the 1950s, whereas the period between 1960 and 1983 received normal to above-normal rainfall. The data suggest drought may have predisposed the system for rapid rates of woody plant invasion in the post-drought period. However, would a change of this magnitude have occurred if livestock had not been grazing the site and (a) spreading seeds of the dominant woody species (Brown and Archer, 1987) and (b) preventing fine fuels from accumulating and fire from occurring? Conversely, would these activities of livestock have produced this change even if the drought had not occurred? It is likely that livestock, fire, and climate interacted to produce the observed change. However, it is difficult to rank their order of importance.

How might the relative contributions of these interacting factors be determined? In a unique field study in Utah, Madany and West (1983) have documented a case in which a savanna protected from cattle grazing was maintained, whereas nearby edaphically similar sites subjected to cattle grazing changed from savanna to dense woodland soon after the introduction of livestock in the late 1800s. Low frequencies of fire were documented on the savanna site protected from grazing, indicating that frequent fire was not required to maintain the grass-tree balance in this system. Both sites experienced the same climate, yet one changed

dramatically over 100 years, whereas the other did not. Such data indicate that livestock grazing has been the proximate cause of vegetation change on this site, not changes in fire or climatic regimes. Although climatic fluctuations in recent history may have been necessary to have caused the change on the grazed site, they were not sufficient to cause change on the ungrazed site.

Goldberg and Turner (1986) examined vegetation composition in permanent plots established as early as 1906 in a variety of habitats in the Sonoran Desert of southern Arizona. The woody vegetation composition in these plots, which were protected from grazing, did not exhibit consistent, directional changes. Thus, in the absence of grazing by livestock, climate has failed to produce a successional change in vegetation structure in this ecosystem.

Figure 24.8 depicts a fenceline contrast in central Australia. The properties on both sides of the fence have similar soils, have experienced the same climate, and have the same general history of livestock grazing. However, prickly acacia (*Acacia nilotica*) plants from Africa were introduced along water courses on the property to the left of the fence in the 1940s. At the time of this photograph, taken in 1988, prickly acacia had spread throughout the pasture and formed dense stands. The plant was not introduced to the property on the right. The fact that the spread of the plant has been limited by the fence suggests that livestock rather than native fauna are the principal agents of seed dispersal. Field observations indicate that seed production and seedling establishment of prickly acacia away from watercourses is episodic, occurring only during periods of sufficient rainfall which are infrequent and widely spaced (Burrows, et al., 1990). Thus, while climatic variables are a key component in dictating the dynamics of the spread of this plant, they cannot account for the differences in vegetation structure on these adjacent properties.

24.5 SUMMARY

One of the challenges facing ecologists today, is that of understanding ecosystem processes well enough to recognize fluctuation associated with natural climatic variability and distinguish it from directional changes associated with human exploitation, activities of native fauna, or changes signaling a transition into new climatic regimes. Climatic phenomena, ecosystem processes, and human activities interact and are interdependent upon one another (Fig. 24.9). Controversy surrounding the supposition that increasing CO_2 in the atmosphere is causing changes in global climate (Idso, 1984; Cess and Potter, 1984; Reifsnyder, 1989) is largely caused by the way assumptions regarding process controls and interactions are handled.

Climatic processes and events clearly influence human activities directly via extreme events such as drought, floods, hurricanes, and tornadoes. In other instances the effects of climate on human activity may be realized indirectly via the influence of climate on ecosystem processes which control productivity and species abundance and distribution. At the same time, human activities may influence climatic processes either directly or indirectly. Industrial and land use practices have increased concentrations of greenhouse gases (CO_2, CH_4, N_2O, CFC's, etc.) and have reduced stratospheric ozone, creating the potential for climate change (Boden et al., 1990). Human

Climate Change
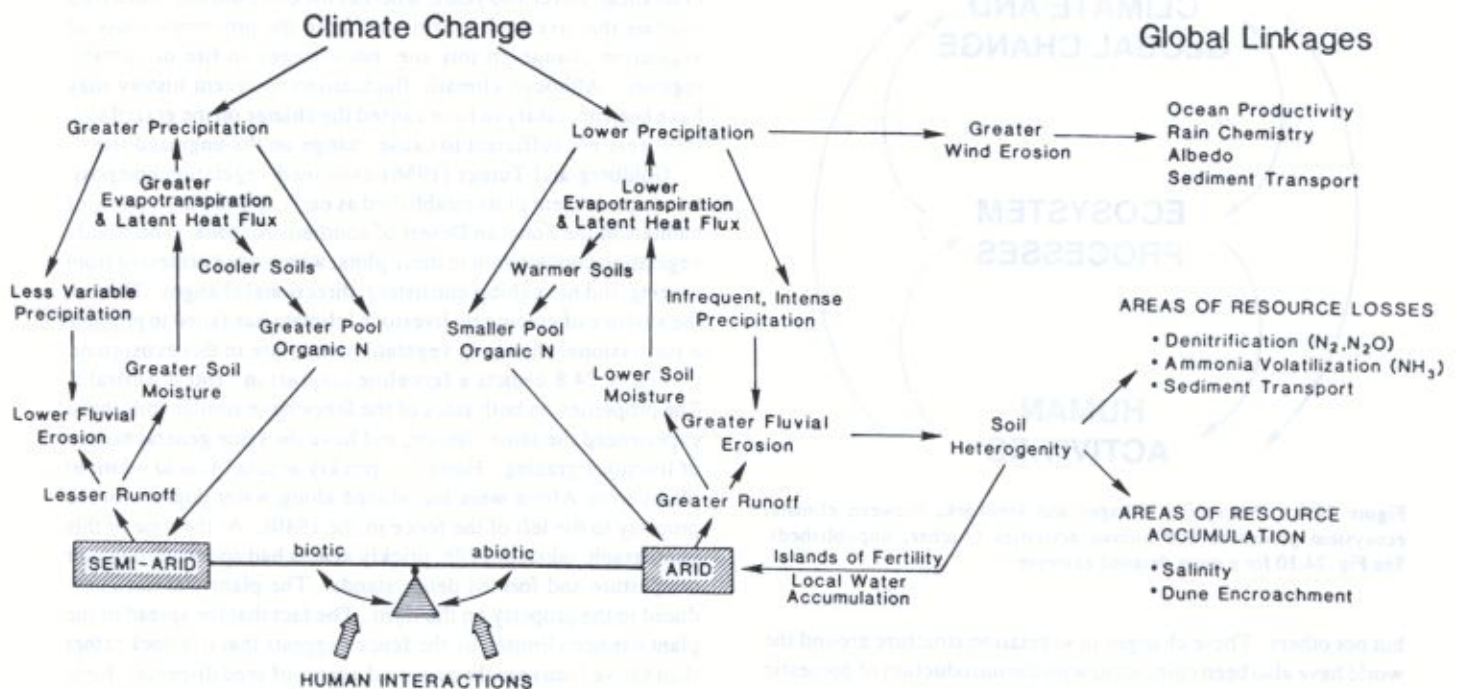
Global Linkages

Figure 24.10. A model illustrating how biological feedbacks and potential changes in ecosystem properties during desertification may be linked to changes in climate and global processes (from Schlesinger, et al., 1990; reprinted by permission of AAAS).

activities also affect climate indirectly via their impacts on ecosystem processes. Deforestation and grazing, for example, influence species composition, primary productivity, and organic matter decomposition, thereby altering the liberation and sequestering of CO_2. Changes in land cover and ecosystem processes may further influence climate by altering surface energy flux and biophysical properties (albedo, temperature, evapotranspiration, air circulation, etc.) and by changing levels of particulate input (e.g., dust) into the atmosphere (Pielke and Avassar, 1990, Bryant, et al., 1990, Graetz, 1991). The linkage of these various processes at local and regional levels may eventually be manifested at global levels (Fig. 24.10).

Correct representations of ecosystem processes have potential for substantially improving the performance of global and mesoscale circulation models. However, for this to occur, ecologists must "scale up" research in time and space to address regional processes which provide critical inputs to climate models. This will require development and integration of new paradigms, new techniques and approaches in modeling and remote sensing and extensive collaboration with atmospheric scientists and climatologists. Research on this topic must also consider human activities, both as they contribute to and as they are affected by global environmental change (Brown and Roughgarden, 1989, Jacobson and Price, 1991; Schimel et al., 1991).

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