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GRADIENT ANALYSIS OF ECOLOGICAL CHANGE IN
TIME AND SPACE: IMPLICATIONS FOR
FOREST MANAGEMENT

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Abstract. Gradient analysis is a powerful technique to analyze for, and detect change in, the dynamics, structure, and function of ecosystems. Boundaries between zones or communities occur at distinctive locations along environmental gradients and are expected to be especially sensitive to environmental change. Gradient analysis can be performed at a range of scales, and allows integration and extrapolation of change across scales from those associated with communities to those of biomes.

This review outlines the properties of gradients in space and time and uses an example of forests in the Rocky Mountain Physiographic Province to demonstrate constraints, the complex mosaics associated with distributional limits, transfers across boundaries, the role of disturbance, and threshold dynamics. A climate-change scenario is developed to hypothesize future changes in boundary movements, community mosaics, and ecosystem properties along elevational and latitudinal gradients in the Rocky Mountain Province.

Mechanistic explanations of ecological phenomena that are necessary for management require information on: (1) the physical environmental constraints operating on the ecosystem; (2) the biota that operate within those constraints; and (3) the interactions among the biota and between the biota and environment. The relative importance of these three elements differs between environments and along environmental gradients. Biota and their interactions may account for much of the variance in system structure and function in mesic environments, while abiotic factors may limit biotic activity in less-favorable (arid) habitats. Plot studies that are analyzed as points along broader scale environmental gradients can provide quantitative information on the major driving variables, and broad-scale analyses of environmental factors along the gradient generate the information for extrapolating between sites and across scales. Modeling that includes such spatial gradients provides the foundation for local to regional management programs.

Key words: climate change; ecotones; gradient analysis; landscape mosaics; Rocky Mountain forests; threshold dynamics; watershed dynamics.

INTRODUCTION

Gradient representation has become a standard technique for the examination of vegetation patterns, and has enhanced our understanding of the environmental control of ecosystem structure and function. The approach to the understanding of communities and ecosystems through analyses over gradients permits us to study the way gradients of species populations and community characteristics change in response to, or in concurrence with, gradients of environment. The approach that relates gradients to one another on three levels—environmental factors, species populations, and community characteristics—is termed "gradient analysis" and is a major alternative to approaches to communities through classification (Whittaker 1973).

Changes of vegetation along altitudinal gradients in mountains are observed throughout the world. The description of these changes in the form of "life-zones" by C. H. Merriam was one of the early developments in ecology. The zones are the kinds of communities humans recognize, mainly by their dominant plants, within the continuous change of plant populations and communities along the elevation gradient. The zones can be compared to the specific colors humans recognize and accept as useful concepts; however, the real understanding comes from recognition that the spectrum is continuous (Whittaker 1973). Changes in the locations of these "life-zones" along gradients over time are likely to result from changes in environmental factors, e.g., climate change. Such changes may be best identified at the boundaries of the zones (i.e., ecotones and transition zones), where gradients are relatively steep. di Castri et al. (1988) point out that the recent widespread recognition of and call for the study of...
ecotones are based on the following four suppositions: (1) the number of putative characteristics of ecotones that are significant in understanding ecological systems in general; (2) the assumption that ecotones are highly sensitive, and thus, are good early indicators of changes along gradients; (3) the potential significance of ecotones for prudently managing the biosphere; and (4) the recognized relative paucity of data from ecotones.

Gradient analysis also can be used at broader scales: regions and continents. Gosz and Sharpe (1989) discuss the approach of evaluating the broad-scale environmental gradients that occur over a region and identifying boundaries or transition zones that occur in the relatively steep portions of those gradients. At the scale of regions, the boundaries are likely to be those of biomes or dominant life-forms, and the environmental driving functions causing those gradients are likely to have significant effects on ecosystem-level processes. Many transitional areas are important globally and extremely sensitive to broad-scale changes such as climate change and human activity (e.g., desertification, Davis 1988). Studies on the steep gradients associated with biome boundaries will be especially important in establishing: (1) gradient relationships with distance (e.g., latitude); (2) the scale-dependent or scale-independent nature of spatial variability; (3) the influence of gradient steepness on system properties; and (4) integrated responses across the region (Gosz and Sharpe 1989). These objectives form the core research program for the Sevilleta Long Term Ecological Research (LTER) area in New Mexico where studies are being performed across spatial/elevational gradients. The next section discusses a number of ecological properties and processes along typical gradients in western forests.

**Gradients in Space**

**Gradient analysis in Rocky Mountain forests**

Peet (1978) presented a detailed gradient analysis of western forests along a latitudinal sequence of the southern Rocky Mountain Physiographic Province. The study documents community dominance along the east slope of the southern Rocky Mountains extending from the Laramie Range in southern Wyoming south to the terminus of the Sangre de Cristo Mountains east of Santa Fe, New Mexico (41°20' N to 35°30' N, Fig. 1). This 500 km long gradient along the eastern slopes of the mountain axis forms an ideal area for examining latitudinal and elevation variation in vegetation. The study documents the interaction of gradients of latitude, moisture, and elevation in the determination of local- to regional-scale patterns in community composition. Mosaic diagrams represent the vegetational variation relative to elevation and moisture gradients for a latitudinal sequence at four sites (Fig. 2).

The diagrams depict the boundaries (i.e., ecotones) of vegetation associations and their environmental limits. These are essentially constraint envelopes of physical, chemical, and biotic conditions within which the systems must operate. Such constraint envelopes have considerable predictive power (O’Neill et al. 1989). We can state with assurance that a system is within a constraint envelope, and changes in the position or location of the envelope will cause changes in the position or location of contained communities. Studies focused at these “edges” can more easily show the relation of environmental changes to biological changes.

The mosaics of Fig. 2 are excellent examples of how the biotic responses to certain gradients change over the region. Boundaries that are near vertical reflect a community whose distribution is very sensitive to changes in the moisture gradient (e.g., Fig. 2A: *Abies concolor*–*Pseudotsuga*, *Pinus flexilis*, *Pinus aristada* of the Sangre de Cristo Mountains, New Mexico). Boundaries close to horizontal reflect distributions sensitive to elevational (e.g., temperature) differences (e.g., alpine timberline). Comparison of the four mosaics shows differences in the constraint envelopes over the latitudinal gradient. These differences are fundamental to predictions of gradient dynamics for factors such as climate change, fire disturbance, etc., which are discussed later.

All of the dominant tree species of these western forests can play a successional role; however, only *Pi-
Fig. 2. Vegetation diagrams indicating the distribution of forest types relative to elevation and moisture gradients for four study sites in the Southern Rocky Mountain region. Forest types are characterized by the dominant tree species present. The potential distribution of successional forest types is indicated with ——— for *Populus tremuloides* dominance, and — — — for *Pinus contorta*. Species abbreviations used are Abco = *Abies concolor*, Abla = *Abies lasiocarpa*, Pien = *Picea engelmannii*, PiFl = *Pinus flexilis*, Pipo = *Pinus ponderosa*, Pipu = *Picea pungens*, Poan = *Populus angustifolia*, Potr = *Populus tremuloides*, and Psme = *Pseudotsuga menziesii* (from Peet 1978).
**Fig. 3.** Biome transition zone, reflecting the increased fragmentation of the community mosaic at finer scales. Fragmentation also increases with distance from the core, through the transition, due to increased sensitivity to microsite conditions at the edge of species' ranges (from Gosz 1991b).

*Pinus contorta* and *Populus tremuloides* are primarily successional. The high fire frequency of the region causes these species to dominate most middle-elevation forests, either together or separately. The latitudinal gradient demonstrates the change in dominance between the two types. In the north, *Pinus contorta* is more competitive and by competitive displacement forces *Populus tremuloides* to the exterior portions of its constraint envelope (Peet 1978). The southern terminus of the range of *Pinus contorta* occurs in the vicinity of the Spanish Peaks area (Fig. 2B). Here, the pine is confined to sheltered, north-facing slopes between 2800 and 3100 m. *Populus* becomes the dominant successional species over most of the remaining middle-elevation slopes. An interesting aspect is that despite the continuous decrease of *Pinus contorta* dominance from north to south, at the terminus of its range the species still occurs in monospecific stands. The species appears to occupy progressively smaller areas while retaining dominance. This pattern of decreasing patch size at the edge of a species distribution (i.e., edge of the constraint envelope) should be a common pattern (Neilson et al. 1989, Gosz 1991b).

A parallel pattern occurs on Pikes Peak, where *Pinus contorta* is absent. Most likely, this eastern outlier historically has been subjected to climatic conditions that were too dry to support *Pinus contorta*. Here, *Pinus flexilis* has expanded its niche to fill the successional role of *Pinus contorta*, and appears to have preempted many potential sites from *Populus tremuloides* (Peet 1978).

**Mosaics across boundaries and ecotones**

The mosaic diagrams of Fig. 2, biome maps, species distributions, etc., are somewhat misleading in that they represent the edge of a classification unit as a line. All of these transitions, however, commonly take on the form of a complex mosaic. Fig. 3 is a schematic diagram of a hypothetical biome transition reflecting an increased fragmentation of patches at finer scales (Gosz 1991b). This sequence also can be used to represent changes in the mosaic with distance away from the core area. Neilson et al. (1989) and Neilson and Wullstein (1983) describe this phenomenon as an increased sensitivity to microsite conditions, as Peet (1978) did for *Pinus contorta*. When the regional climate is near optimal for a given set of species (i.e., well within the constraint envelope), minor differences between microhabitats will be within an organism’s range of tolerance. A given species can range over a variety of slopes, aspects, and elevations, resulting in large patches of the species. Where the regional climate is marginal, many microhabitats are outside the species' range of tolerance, resulting in its distribution being constrained to fewer microhabitats of smaller size. Thus, the response of a species to environmental factors is amplified or attenuated across the transition zone, and the different microsite characteristics offer significant
information about environmental influences at the species level. The microsites are likely to be extremely sensitive to change, and patterns in substrates (e.g., soils, microtopography) can control mosaic patterns and dynamics.

Grover and Musick (1990) provide excellent empirical evidence for these changes in the mosaic with their study of desertification and increased dominance by desert shrubs in southern New Mexico. The boundary of the desert shrub zone moved northward over the recent 50-yr interval, and there was an increase in the proportion and size of habitats occupied by the desert shrub community (Fig. 4). The patterns of Figs. 3 and 4 are typical of most "edges" and are expected to move over the landscape in response to shifts in climate or other environmental factors. The nonlinear aspects of such dynamics are discussed later (see Temporal changes . . .; Threshold dynamics, below).

**Transfers in landscapes**

The configurations of patch sizes and juxtaposition that occur over gradients have profound effects on the types and distributions of animal and plant communities that can be supported (Forman and Godron 1986). Some animals forage among different patches, while others are confined to single patch types. Thus, movements of organisms, propagules, and disturbances across the landscape are affected. Some mosaic patterns hinder the movements of particular entities while promoting the movements of other entities. The patterning of resources on the landscape is a predictor of the scales at which organisms must operate to utilize the resources and thereby affect transfers. As the distribution and pattern of the resource change (either over space or through time), so also the scale of utilization must change (O'Neill et al. 1988). If a resource is randomly distributed, an organism must operate at a sufficiently large scale to avoid being restricted to a portion of the total landscape. An organism must adjust its resource utilization scale if a resource is contagiously distributed. In general, as the resource becomes more highly clumped, it becomes clustered into fewer portions of the landscape. The organism must then be able to operate at broad scales to move from one resource patch...
to the next. Because organisms differ in utilization scales, communities should show distinct patterns, with dominants operating on fine scales and subdominants operating at broader scales. Similar generalities result from considering that landscapes must contain a minimal percentage of specific vegetation cover to serve as suitable habitat for particular organisms (O’Neill et al. 1988). As the landscape mosaic changes, thresholds might be reached where sudden changes in movement patterns will take place.

Wiens et al. (1985) developed an analogy of boundaries between elements in a landscape to membranes in organismal or physical systems. Like membranes, boundaries vary in their permeability or resistance to flows. This variation is a consequence of characteristics of the boundary itself (e.g., thickness, disparity between separated patches) and of the responses of different materials, organisms, or abiotic factors to the boundary. Thus boundaries can be impermeable to transfers of some materials but can be permeable or leaky to other fluxes. Abiotic vectors such as wind and water are strongly affected by features of the physical structure of the boundary. Wind movements across a boundary between a patch with low, sparse vegetation and one with greater vertical structuring and coverage, as occurs at some grassland–shrubland or grassland–tree boundaries, will be altered by the increased turbulence and decreased velocity produced by the more structured plant canopy.

Johnston and Naiman (1987) derived two generalities regarding influences of abiotic vectors on landscape boundary dynamics. First, the permeability of a lateral boundary to abiotic vectors is a function of the kinetic energy of the vector; both wind and water have higher transporting capacities at higher velocities. Second, within-patch retention is maximized by a rapid decrease in kinetic energy of the vector. For waterborne transfers this would occur where the patch boundary coincides with a decrease in slope, such as the boundary between an upland stream and a beaver impoundment. For wind-borne transfers a decrease in kinetic energy would occur where there is change in vertical structure, such as the edge of a forest.

Watersheds are excellent integrators of biogeochemical processes as well as being sensitive to change (Dahm and Molles 1991). A long-term study of a series of watersheds within the Tesuque Watershed study area near Santa Fe, New Mexico, provides hydrologic data that demonstrate the effect of an elevational gradient (i.e., temperature, precipitation) on stream ecosystems and on the dynamics of transfers through the landscape. The watersheds occur in the Sangre de Cristo Mountains and have vegetation ranging from pinon–juniper to spruce–fir and alpine tundra (Figs. 1 and 5; Gosz 1978, Peet 1978). Data reported in Dahm and Molles (1991) characterized the forested watersheds from mixed conifer to spruce–fir/alpine. The highest watershed (3231–3734 m) is dominated by spruce–fir (Picea engelmannii–Abies lasiocarpa var. arizonica) with mean precipitation of 859 mm during 1972–1980 (Fig. 5: 15). The intermediate watershed (2950–3525 m) is dominated by aspen (Populus tremuloides) and mean precipitation was 705 mm during the same period (Fig. 5: AW1). The third watershed used in this contrast (2804–3444 m) is dominated by mixed conifer forest and had a mean precipitation of 578 mm (Fig. 5: 5).

The gradient of decreasing moisture with decreasing elevation is accompanied by an increasing nonlinear response in annual stream flow from these watersheds (Fig. 6). The regression analysis for the highest watershed demonstrated that discharge increased or decreased \( \approx 1.6 \% \) for each 1% change in precipitation, while total precipitation varied by a factor of two during the period of measurement. This high-elevation watershed displayed a flow response characteristic of watersheds in mesic environments (Nemec 1986). The intermediate aspen watershed showed annual discharge to increase or decrease \( \approx 2.4 \% \) for each 1% change in annual precipitation; the amount of change in flow response to a change in mean annual precipitation was
greater than in the higher elevation watershed and the response was more variable, although a linear response was still apparent.

The lowest watershed used in this comparison demonstrated a nonlinear response in stream flow with variations in precipitation. Relatively small increases or decreases in precipitation yielded large changes in total annual flow. The pattern of the three watersheds conforms to results obtained by Nemec (1986) for gradients from mesic to semi-arid environments. The degree of amplification increases as the sites become drier and semi-arid conditions are encountered. Molles and Dahm (1990) also demonstrated this amplification with other forested basins in New Mexico. They showed that spring discharge from two rivers (Pecos River, Gila River) was strongly influenced by the El Niño and La Niña extremes of the ENSO (El Niño Southern Oscillation) phenomenon. Mean spring runoff was 6.0–7.4 times higher in El Niño years in spite of the fact that differences in precipitation were only 2.1–2.8 times higher in those El Niño years. The amplification phenomena demonstrated by forests along elevational gradients in these semi-arid regions will be valuable tools in quantifying changes in climate.

**Disturbance dynamics**

Disturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). Many examples illustrate that environmental gradients lead to the landscape heterogeneity that plays a key role in the spread of disturbance. The spread of disturbance across a landscape is an important example of a functional characteristic that is influenced by spatial heterogeneity (Turner et al. 1989). In general, greater heterogeneity inhibits disturbance spread (Forman and Godron 1986), and the spread of disturbance decreases as boundary-crossing frequency increases, that is, crossing a boundary into a patch that retards the spread. This occurs with reference to animal movement as well as to disturbance spread in a landscape. In addition, edges can act as barriers to or filters for the spread of disturbance, due to the special structure or combination of species present in an edge.

In some instances, landscape heterogeneity may enhance the spread of disturbances (Franklin and Forman 1987, Turner and Bratton 1987). This discrepancy forces distinguishing two types of disturbances: (1) those that spread within the same cover type (e.g., species-specific pest in a forest); and (2) those that cross ecosystem boundaries and spread between different cover types (e.g., fire spreading from grassland to forest). If the disturbance is likely to propagate within a community, high landscape heterogeneity can retard the spread of the disturbance. If the disturbance is likely to move between communities, increased landscape heterogeneity can enhance the spread of disturbance. The rate of disturbance propagation should be directly proportional to landscape heterogeneity for disturbances that spread between communities, but inversely proportional for disturbances that spread within the same community (Turner et al. 1989). Landscape configuration (i.e., spatial juxtaposition of patches, corridors, and matrices) can be a controller of disturbance spread because it determines boundary-crossing frequency (Forman 1987).

Future changes in environmental gradients are likely to cause altered mosaics and complex dynamics in the frequency and spread of disturbance. Fire is a major disturbance agent in western forests, and National For-
ests in the Southwest lead the nation in average number of lightning fires and area burned by these fires each year (Swetnam and Betancourt 1990). The extensive fire regime in this region occurs as a result of intense lightning storms during the summer months. The interannual variations in fire activity probably derive from the influence of winter-spring precipitation on the accumulation and moisture content of the fuels. Swetnam and Betancourt (1990) used fire-scar and tree-growth chronologies (1700–1905) in Arizona and New Mexico to show that small areas burn after wet springs in association with the low phase of the Southern Oscillation (SO), whereas large areas burn after dry springs in association with the high phase of the SO. Climatic change resulting in altered cool-season precipitation in this region is expected to affect the incidence of fire frequency, its extent, and the magnitude of disturbance. Fire frequency in Wisconsin apparently changed by an order of magnitude between the Little Ice Age and the present (Grimm 1984, Neilson et al. 1988). It is uncertain how the Southern Oscillation may change in future climates; however, assuming that the high phase (reduced cool-season moisture) occurs more frequently, the increased probability of synchronous, large fires will influence the landscape mosaic of patches recovering from such disturbances.

Knowledge of the scale of vegetation units generated by fire is fundamental to resolving views of ecosystem dynamics (Heinselman 1981). If the patches in a mosaic are large, then studies designed to look at system processes must encompass enough patches to sort out the time-related factors that explain differences between patches. The total area of a burn influences re-vegetation from seed sources outside the burn. The effect is modified by the shape and alignment of the burn with respect to land forms, and by unburned inclusions. The interference interval is a regulator of fuel and fuels characteristics. Short periods allow little time for new fuels to develop; however, partial consumption by previous fires allows important carryover fuels.

Several aspects of altered climate may influence fire-caused mosaics in different ways: (1) Increased drought frequency may decrease the interference interval; (2) Increased drought frequency may increase the general patch size of the mosaic (this may not be sustained if a shorter interference interval reduces the fuel necessary for large burns); and (3) Prompt postfire vegetation establishment may be delayed if the local climate has become unfavorable for the local seed source.

Anthropogenic influences can reduce or amplify the potential fire changes from altered climate. Fire control, logging, land clearing, roads, and urban areas greatly modify natural fire regimes. On the other hand, a large proportion of fires is human-caused, and the higher fire risk associated with drought may be realized by human use of these forests.

It is generally acknowledged that pest infestations can change dramatically with increased CO₂ levels and climate change. These dynamics are difficult to predict; however, changes in carbohydrate-to-nitrogen ratios of plants and changes in rainfall and temperature patterns are almost certain to change the kinds and severity of diseases and pests. For example, a drier climate and more water stress, as projected for much of the Western United States, are likely to increase attacks by boring insects (Kramer and Sionit 1987). Species that currently are not pests are likely to become pests, and current pests may decrease in influence. These disturbance dynamics may interact significantly with fire disturbance dynamics and influence the spatial patterns of the resulting mosaics.

**Temporal Changes in Gradient Patterns**

The previous sections discussed the general properties that vary in complex ways over gradients of environmental factors. Environmental constraints vary spatially and can cause variable patterns of change over distance. The sharp transitions (e.g., boundaries) that occur along gradients may be caused by steep gradients in environmental properties on certain areas or by threshold phenomena on certain portions of the general gradient. Threshold dynamics are expected to occur near boundaries (Gosz and Sharpe 1989); however, they also may occur over much of the landscape (boundaries in time). This section discusses these rapid temporal dynamics and their influence on spatial characteristics and on forest ecosystem properties.

**Threshold dynamics**

Biological systems are metastable (O'Neill et al. 1989). This means that the properties of the landscape remain stable only over a limited range of conditions. When those conditions reach a critical threshold, the system may reach a discontinuity (i.e., a bifurcation) resulting in a radical change in the system state. Bifurcations may underlie unexpected or surprising phenomena observed in landscapes, and examples are available from a diversity of systems. Jones (1977) suggests that pest outbreaks are a result of such dynamics, and Worden and Donaldson (1987) and Rozich and Gaudy (1985) reported that bifurcation dynamics must be incorporated into models for microbial transient responses. Crowley and North (1988) argue that bifurcation phenomena may be responsible for climate changes such as transitions between glacial and interglacial periods.

A transition zone along an environmental gradient is hypothesized to have properties different from the adjacent habitat types and may amplify or attenuate certain system processes such as productivity, resource dynamics, and availability (Naiman et al. 1988, Gosz and Sharpe 1989). In terms of system dynamics, boundaries are locations where the rates of ecological transfers (e.g., energy flow, nutrient exchange) change...
abruptly in relation to those within the more homogeneous units on either side (Weins et al. 1985, Gosz 1991a). Chaos theory, a mathematical concept predicting unpredictability, has been suggested to model such variability in transitions (Naiman et al. 1988, Gosz and Sharpe 1989). The premise of chaos theory is that chaotic, or seemingly unpredictable, behavior is a special manifestation of an underlying structure. Naiman et al. (1988) found that such models predict that boundaries can behave in ways that are not simple averages of adjacent resource patches. Such “emergent” properties are more likely to occur where there are: (1) contrasting life-history strategies or life forms on each side of the transition; (2) different constraints operating on organisms of each biome; (3) different scale-related features in the two biomes; and (4) different heterogeneity features (Hansen and Urban 1991). Emergent properties may be a result of the magnitude of contrast between adjacent areas as well as of increased heterogeneity of patterns in the transition zone. Such amplification or attenuation can magnify the biotic response to environmental dynamics. Gosz and Sharpe (1989) described a cusp catastrophe model with characteristics that fit observed phenomena in semiarid regions relating primary production, a precipitation threshold (Sala et al. 1988), and the inverse texture hypothesis (Noy-Meir 1973). Characteristics of the model were: (1) bimodality—the system at low precipitation levels tends to be either in one state or another; (2) discontinuity (catastrophe)—a rapid change or jump from one condition to another; (3) hysteresis—the path that the response makes as the controlling factors move in one direction is different from the response as the controlling factors move in the opposite direction; and (4) divergence (bifurcation)—small differences can cause paths of change to diverge markedly.

An important question is whether bifurcation phenomena can be predicted. If measurable characteristics of the dynamics of the system on short time scales can be identified that anticipate impending bifurcations, they could play a major role in monitoring landscape and ecosystem changes. O’Neill et al. (1989) discussed observable phenomena that could be useful in detecting the instability near such bifurcation points: (1) increases in the relaxation time from all perturbations which could be measured directly; and (2) increases in the variance of observed fluctuations before the discontinuity (Fig. 7). As the landscape moves toward a critical threshold, variability and local relaxation time may serve as measurable warning signs.

Glass et al. (1988) provide the basis for a mechanistic explanation for such chaotic behaviors in physiological systems that also may apply to ecosystems. It is known that many physiological variables display complex fluctuations in time which are not easy to characterize. Biological systems have many feedback mechanisms, operating simultaneously, that work to maintain key physiological variables within normal limits. In these feedback loops there are delays that are associated with the time interval between the sensing of some disturbance and the development of an appropriate physiological response. The magnitude of such delays can vary widely. Glass et al. (1988) have demonstrated that as few as three feedbacks with different response times can produce chaotic behavior. They suggest that many fluctuations can be due, at least partially, to chaotic dynamics that arise as a consequence of these multiple feedback mechanisms in the nonlinear physiological control systems. An interesting observation to emerge from recent theoretical and experimental studies is that increasing the time delays in feedback systems appears to increase the magnitude of the dynamics. Thus, experimental manipulation of the parameters of the control function could be correlated with observed bifurcations of the dynamics. Another approach is to investigate the effects of blocking some feedback loops but not others. To my knowledge, this experimental approach has not been investigated at the ecosystem/landscape level.

Climate-change scenarios

Scientists agree, by and large, that there is mounting evidence that significant warming will occur that will bring new and different climatic regimes. It is anticipated that such changes will affect agriculture, forestry, livestock, water, transportation, energy use, building construction, and many other aspects of human life (Roberts 1987). Basic agreement includes:

Carbon dioxide and other trace gases are accumulating in the atmosphere;

Trace gas accumulation will cause a gradual warming of the average global temperature of between 1.5 and 4.5°C by sometime in the next century;
With gradual warming will come a change in patterns of wind, rain, snowfall, and other elements of climate; there will be considerable regional climatic variability, with some regions becoming warmer and drier, others warmer and wetter, and some perhaps even cooler because of the influence of oceans (Roberts 1987).

Scientists also agree that there are many uncertainties that make predictions difficult at best. It is probable that the overall change will consist of many regional changes of more extreme magnitudes affecting small areas based on local environments. Local changes will be apparent in temperature, cloudiness, overall precipitation, seasonal distribution of precipitation, humidity, soil moisture, wind direction and speed, storm frequency, and length of growing season. Averaged, these local changes will equate to the slightly warmer total global temperature. The following discussion is not as much a prediction as it is an exercise in the evaluation of logical scenarios for warming trends in western forests. The assumptions are relatively simple and they do not account for the complex feedback reactions that undoubtedly will occur. The exercise is directed toward how environmental gradients may change temporally and spatially and how transitions (e.g., boundaries) are likely to respond. Such scenarios may not be useful for current planning purposes. Their primary utility will be in providing a basis for performing preliminary impact assessments. In some cases the scenarios may allow some users to evaluate risks associated with changes or decisions based on such changes.

Boundary movement.—The scenarios developed for the environmental gradient in the Rocky Mountain region are based on the analyses of Peet (1978; Fig. 2) and Leverenz and Lev (1987). Leverenz and Lev projected changes in the natural ranges of conifer species based on knowledge of plants' responses to increased temperature and decreased site water balance, combined with a climatic scenario assuming a doubling of atmospheric CO₂. In the Rocky Mountain region (see Fig. 1), ponderosa pine, Douglas-fir, and Engelmann spruce should decrease in area while the net effect on the species occupies a relatively small portion of the habitats.

Ecosystem properties.—The potentially complex array of changes along western forest gradients is likely to lead to an equally complex set of altered ecosystem properties. I feel some of the most obvious changes will be those resulting from elevational shifts in these forest communities. The following discussion provides several examples.

As species move to higher elevations following climate warming, the amount of habitat area decreases (assuming the lower elevational limits move upslope as well). Therefore, properties characteristic of certain vegetation types (e.g., spruce-fir) will be less influential on the change in discharge, particularly those of floods and droughts, have profound effects on the function of stream ecosystems and their associated riparian communities, on the structure of stream communities, and on the dynamics of stream populations (Molles and Dahm 1990). Flow plays a central role in stream ecology because discharge controls many key chemical and structural attributes and integrates complex environmental conditions. Drying, as a disturbance, has received less attention than flooding, but similar disruptions of the function, structure, and dynamics of stream ecosystem communities and populations have been reported.

Vitousek et al. (1982) reported on the controls of potential N mineralization, nitrification, and nitrate mobilization in a wide range of forest ecosystems, including the ponderosa pine, mixed-conifer, aspen, and spruce-fir ecosystems on the Tesuque Watersheds of...
New Mexico. Ponderosa pine and spruce–fir had low N mineralization and nitrification rates while aspen and mixed-conifer forests exhibited rapid N mineralization and nitrification. A primary conclusion from these studies was that N-poor sites (low N mineralization and low litterfall N) produced refractory organic N compounds and produced litter with high C:N ratios. Additional work (Gosz and White 1986, White and Gosz 1987) identified that low pH in combination with factors associated with organic quality controlled N mineralization and almost completely limited nitrification in spruce–fir soils, while N mineralization in the forest floor of ponderosa pine was limited by low nutrient availability (other than N). The organic quality of the substrate and temporal changes in organic quality appeared to control N mineralization and nitrification processes (i.e., N availability) in forest-floor and mineral soils from all other sites.

As these communities move upslope in a scenario of climate change, patterns in these processes are likely to follow, since they are largely controlled by tissue chemistry of the dominant species in the community. The expansion of the zone of mixed conifer to high elevations (loss of spruce–fir) implies that most of the mountainous regions will have nitrogen-cycling processes characteristic of these mixed-conifer communities. Such a change would be important to timber-harvesting management, since greater losses of nitrate via streamwater are associated with forests having rapid N mineralization and nitrification properties (Vitousek et al. 1981).

**Implications for Forest Management**

Managing forests means managing for a broad array of products, services, and values that vary in importance over time and regions. In recent times the concerns of society involve sustainability, maintenance of diversity, and aesthetics (NRC 1990). One of the newly developing initiatives concerns the sustainability of natural and managed systems (i.e., “The Sustainable Biosphere Initiative,” Lubchenco et al. 1991). This initiative recognizes that sustaining Earth’s ecological systems requires an understanding of those systems and calls for basic research to acquire this knowledge (Risser et al. 1991). Managing the biosphere also requires an improved and broadened understanding of the functions of natural and managed systems and incorporation of this knowledge into policy and management decisions that address the concerns of society. In my opinion, the basic understanding of spatial dynamics at many scales, variations in structure and function of ecological systems along environmental gradients, and diversity patterns along environmental gradients are fundamental to this initiative. The previous sections provided examples of dynamics and understanding gleaned from analyses of gradients in time and space.

**FIG. 8.** Hypothetical changes for mosaic diagrams of study areas along the latitudinal gradient in the Southern Rocky Mountain region (see Fig. 2). Light shading indicates *Populus tremuloides* and dark shading indicates *Pinus contorta*. The changes are based on a doubled CO₂ scenario. Species abbreviations used are: Abco = *Abies concolor*, Abla = *Abies lasiocarpa*, Piar = *Pinus aristata*, Pico = *Pinus contorta*, Pien = *Picea engelmannii*, Pipf = *Pinus flexilis*, Pipo = *Pinus ponderosa*, Pipu = *Picea pungens*, Poan = *Populus angustifolia*, Potr = *Populus tremuloides*, Psme = *Pseudotsuga menziesii*.

I conclude this section with a discussion of the role of this approach for management. Mechanistic explanations of ecological phenomena that are necessary for management ordinarily require
information on: (1) the physical environmental constraints operating on the ecosystem; (2) the biota that operate within those constraints; and (3) the interactions among the biota and between the biota and environment. These three elements determine the biotic structure and process rates that occur within an ecosystem. Most of our current knowledge about ecosystem structure and function has been generated from studies on small areas represented by plots. Often it is assumed that climate is constant, and spatial variability has been ignored or removed in the study design. Although an ecological explanation requires all three elements identified above, the relative importance of the elements differs between environments or along environmental gradients. For example, in more-mesic habitats and areas, the favorable abiotic conditions allow the biota and their interactions to account for much or most of the variance in system structure and function. In more arid habitats, physical conditions can be primary constraints on biotic structure and activity. Quantification of gradients of such constraints, from local to regional, provides a powerful tool for analyzing the control of system processes at different scales from within and between geographic regions to microsites within local habitats. Although the classification of habitat types implies uniformity within such units, it is likely that gradients occur, causing a range of structural and functional attributes within each classification unit. A simple comparison between different sites may not allow accurate extrapolation of results between sites or to regional areas.

Woodman (1987) suggests that the greatest technological change most likely to influence future forest management is embodied in the concept of “site-specific” management prescriptions. The complex of environmental and ecological variables that can change along gradients dictates that successful management for sustainability, diversity, etc., include this “site-specific” concept. These site-specific management prescriptions can be related to the broader-scale gradients in the same way that other ecological parameters can. Plot studies can provide valuable information if they are analyzed as points along environmental gradients. The process-level information at a site identifies the major driving variables for ecosystem structure and function, and gradient analysis provides information for extrapolation between sites. Modeling that includes such spatial gradients provides the foundation for local to regional management programs (Burke et al. 1990). The gradient pattern of site-specific management extrapolates to broader-scale management that can account for broader-scale issues such as biodiversity, landscape patterns of matrix and corridors, regional markets, transportation, etc. Site-specific management is not new, nor is “plot-specific” research. Understanding the broad-scale factors that account for the differences between plots and sites, placing them in a regional context, and understanding and managing for the “new” patterns that emerge at this scale have significant potential. The difficulty in integrating site-specific management into regional management is similar to the difficulty in extrapolating fine-scale results into broad-scale patterns. Dissimilar techniques, lack of standardization, poor information management, and poor communication all detract from the ability to scale-up the site-specific information. Thus, site-specific management needs to be balanced with regional (top-down) direction to develop the context or framework for site-specific management. Using the study of Peet (1978; Fig. 2) as an example, the regional pattern was derived by a standardized approach and evaluation of dissimilar sites along the regional gradient. The individual sites show different sensitivities to moisture, temperature, and species interactions that would lead to a range of site-specific plans for sustainability, diversity, and aesthetics. Broad-scale or regional management considerations, for example, could involve maintaining a broad genetic base for a particular species. Kellison and Weir (1987) posed such a recommendation when they suggested supplementing the genetic base of seedling stock with unrelated clones from natural stands and from plantations established from unimproved seed. The purpose would be to continually strive to create populations of new genotypes, appropriate to the range of conditions along the gradient, that will allow succeeding generations to be well adapted to changing conditions and to maintain a broad genetic base in perpetuity. Other site-to-region scenarios could be constructed for issues such as species diversity of planting stock, fire management, and landscape design.

The regional-analysis approach also allows detection of the broad-scale patterns that may be due to changes in climate or atmospheric parameters (e.g., increased CO₂). This would identify transition areas where physiological stresses were increasing and future management may need to address issues such as watershed protection, rather than timber production. Whereas a site-specific management program may need a long period to be confident that slow and subtle changes are occurring on the site, the same subtle changes occurring simultaneously across a large portion of the region (i.e., across many sites) could be diagnosed more rapidly by regional analysis. Such results could be used by individual sites to anticipate and plan for further changes. To make this type of management system efficient, standardized methods are necessary. Indicators of forest condition (e.g., foliar damage, foliage chemistry, growth measures) that provide a consistent view across the region need to be evaluated and adopted. Procedures such as these and the broader perspective that includes gradient analysis can contribute to our understanding of environmental control and management of ecosystem structure and function.
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LITERATURE CITED


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