# Broad-scale concepts for interactions of climate, topography, and biota at biome transitions

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## 1. Introduction

The workshop leading to this volume emphasized the importance of scale on interpretation and understanding of many environmental phenomena. From painful experience we recognize the significance of scale-dependent results and the difficulty in relating or extrapolating those results to different scales. Problems of global change require that analyses and predictions be developed for very broad scales: regions, continents, and the globe. A common approach is to classify an area of study, determine the representative response for each element of the classification (measure of central tendency) and derive an area-weighted result. Delineation of the number of classes in the area, assumptions of uniformity within each class, and subjective location of boundaries are only a few of the difficulties of this approach. Simply multiplying an average by the delineated area the average is assumed to represent is inaccurate for extrapolation (Risser 1986).

We believe that a successful approach is to evaluate the broad-scale environmental gradients that occur over a region and identify boundaries 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. Changes in the environmental driving functions can then be used to model ecosystem responses (Sala *et al.* 1988). Studies on the steep gradients associated with biome boundaries will be especially important in this approach to establish (1) gradient relationships with distance, (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. These research objectives are being pursued on the Sevilleta Long Term Ecological Research (LTER) site in New Mexico, USA.

The Sevilleta site is a transition zone between four biomes. We follow Whittaker (1975) and define biome as the broad-scale grouping of terrestrial ecosystems with similarities in vegetation structure (formation), environment, and animal communities. In principle, the biome should be characterized solely by life-form, but in practice it is classified as a combination of physiognomy and environment. Six broad physiognomic formations are defined by Whittaker: forest, grassland, shrubland, woodlands (mixed tree, shrub, and grass life-forms), semidesert steppe, and desert. Because these formations occur over such a wide range of environments, biome types are classified on the basis of life-form and climate. The four overlapping biomes at Sevilleta LTER include the Mogollon conifer woodland, the Great Plains grassland, the Chihuahuan warm-temperate semidesert, and the Great Basin cool shrub steppe.

Ecological processes and the environmental variables that constrain them vary as a function of

spatial and temporal scales (Delcourt and Delcourt 1987a; O'Neill *et al.* 1986). Therefore, it is important to recognize that gradients in constraining variables occur at many scales. Gradients can be detected in small-scale constraints; microtopographic gradients affect redistribution of moisture from individual rains. Larger topographic gradients, aspect and slope, affect seasonal or annual irradiance and moisture stress. At still broader scales, gradients in precipitation determine regional and continental patterns of primary production (Sala *et al.* 1988). At any of these scales, more than one constraint may be involved, and the suite of constraints may change as the scale is changed (O'Neill, per. comm.). Nevertheless, at every scale the identification of constraining variables and steepness of gradients holds excellent promise for both monitoring and predicting ecological response to change. The way in which the constraining variable is linked to the ecological processes over space and time may or may not be scale-independent. By studying a range of scales, we may come to a better understanding of how processes operating over gradients can be used to predict long-term change. Implicit is the idea that the constraints of interest are limited to certain scales and confounded by constraints at other scales. Quantification of gradients for such constraints provides a powerful tool for analyzing the control of system processes at different scales from between geographic regions to between microsites within local habitats.

Environmental constraints vary spatially and may show variable patterns of change over distance and through time. The trend can be quantified as a gradient: change in the environmental variable per unit change in distance or per unit of time. Where the environmental gradient is shallow, ecological conditions are similar at any two points in space and the constraints explain little of the variance between ecosystem properties at those points. At the scale identified by the areas being compared, the system may be thought of as homogeneous. Where an environmental constraint shows a steep gradient, information about the constraint can be critical in explaining differences in ecosystem structure and function. The steeper the gradient is, the more likely that differences between ecosystems or bio-

mes along the gradient can be explained by the constraining factor or factors. Biological responses to the gradient are likely to be nonlinear and to magnify the effect of the gradient. When the gradient is shallow, substantial spatial distance is needed between study regions to detect significant change in any ecological process that is strongly constrained by that variable. When the gradient is steep or when significant nonlinear biological response results in a discontinuity in biological characteristics, changes in ecosystem properties often are sharply defined and detectable over short distances. This helps explain why many of our community concepts were developed in areas with steep gradients (*e.g.*, in mountainous topography, Whittaker 1975).

The objectives of this paper are to (1) identify concepts related to pattern and process in transition zones where steep gradients are likely to occur, (2) develop sample hypotheses of ecosystem dynamics associated with change in transition zones, and (3) provide examples of techniques and tools that allow measurement and extrapolation to scales appropriate for broad-scale transition zone studies.

## 2. Transition zones as sensitive indicators

There is a growing literature on the role of ecotones in influencing ecological flows (*i.e.*, energy, resources, information) and biodiversity and in detecting change in the global environment (Hansen *et al.* 1988). Ecotones can be defined as transition zones or tension zones and can be sensitive indicators of change. Although ecotones often are associated with relatively fine-scale phenomena (*e.g.*, forest edge, lake edge, patch edge), the concepts can be applied to broader-scale characteristics such as a biome boundary where ecological change may be distributed over many kilometers. The structural features of fine-scale ecotones (hundreds of meters) are likely determined by site-specific characteristics such as soil discontinuities, lake edge, and even fire. Climate appears as a constant across such small distances. Broad-scale transition zones between biomes (*i.e.*, many kilometers) are more likely to be a result of large-scale climatic features working on a
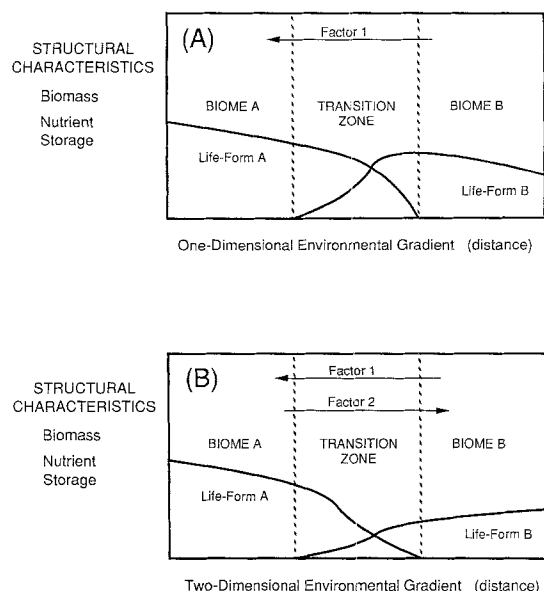
Fig. 1. Structural features that define the transition zone as an association of life-forms from adjoining biomes. A: Structural characteristics expected where biome transition is controlled by a single environmental factor, such as moisture. B: Structural characteristics expected where biome transition is controlled by two or more environmental factors, such as moisture and temperature.

gradient of temperature and moisture (Fig. 1B). The broad-scale change in climate accounts for more of the variation in vegetation across such a transition zone than the fine-scale features of the habitat. Climate has been used by Walker (1981) and Meentemeyer and Box (1987) as the major factor explaining differences in biomass production and decomposition rates for widely separated areas and site-specific factors for differences at the local level. Unfortunately, there have not been comprehensive attempts to understand the probable sensitivity of ecotones or tension zones to projected changes in global environment (Holland 1988).

## 3. Transition zone representation: physiognomic form and ecosystem function

McLaughlin (1986) performed a principal components analysis of flora in the Southwest by weighting all species equally. The analysis demonstrated rather continuous changes in species composition

with distance from the center or 'core' of a biome type (e.g., Great Basin, Chihuahuan Desert). Thus, at the species level, biomes do not demonstrate homogeneity for large areas. Plant life-form (e.g., shrub steppe, perennial $C_3$ grasses, conifer woodland) appears to be a more uniform characteristic over the large area identified with a particular biome. At the broad-scale, biome boundaries are associated with a transition between plant life-forms. Often this is a result of reaching the distributional limits of a generalist species or genus that is capable of extending the full range of the biome (e.g., semidesert shrub Larrea). This results in a steep gradient in plant structural properties and a change in ecosystem process rates at the edge of such distributions.

The structural properties of plants markedly affect ecosystem properties at all scales. Structural differences in leaves (e.g., lignin, protein) affect decomposition and nutrient cycling characteristics (Gosz 1981; Berg and McClaugherty 1987), and woody shrubs and trees markedly affect properties such as ecosystem biomass, nutrient storage, and microclimate (Odum 1971). A primary difference among the various life-forms reflecting different biomes is the magnitude and number of lignified structures and the ability to develop vertical structure, a third dimension. The greater biomass also is associated with increased longevity and an ability to withstand high-frequency, low-intensity fluctuations in environmental conditions (Woodward 1987). On the other hand, greater biomass has increased vulnerability to low-frequency, high-intensity fluctuations. For example, the extended 1950's drought killed many of the Juniper individuals from the Mogollon conifer woodland biome growing at their distributional limits, allowing Larrea shrubs from the semidesert biome to extend its boundaries. A low-frequency, high-intensity cold period with ample soil moisture is hypothesized as a necessary condition to permit the conifer woodland biome to re-establish its 1950 boundary. Thus, the different life-form representatives from different biomes have been observed to react differently to a given change in the environment, in some cases causing a change in local biome boundaries.
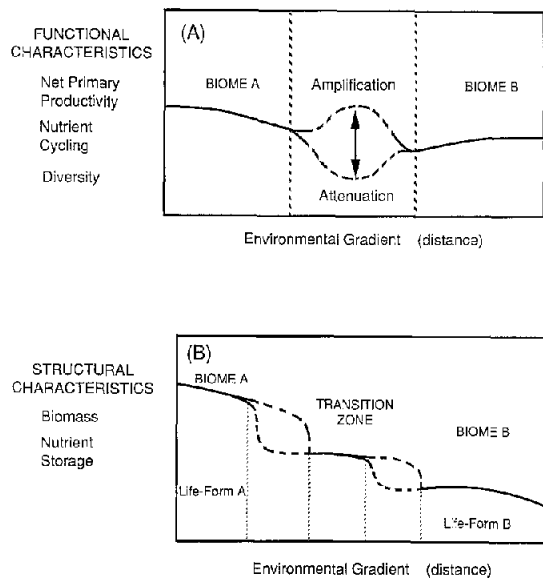
Mixtures of life-forms and species in a tension

FUNCTIONAL
CHARACTERISTICS

Net Primary
Productivity

Nutrient
Cycling

Diversity

Environmental Gradient (distance)



STRUCTURAL
CHARACTERISTICS

Biomass

Nutrient
Storage

Environmental Gradient (distance)

*Fig. 2.* A: The transition zone ecosystem, which is hypothesized to develop unique characteristics and to be very responsive to changing environmental constraints because it is in tension. B: Instability at two edges of biome transition zone (see Section 4.3.).

zone suggest questions of nutrient dynamics and limitation. Nutrient limitation in ecosystems has been noted in many studies while others clearly indicate that each species responds individually to resource availability in relation to its requirements (Chapin and Shaver 1985; Gutierrez and Whitford 1987; Chapin *et al.* 1986; Tilman 1982). The tension zones may be intermediate in resource dynamics in proportion to the mixture of life-forms or may demonstrate amplified or attenuated responses (*i.e.*, nonlinear responses, Figs. 1 and 2). These potentially interesting responses may be extremely valuable measures of the 'pulse' of environmental change.

## 4. Ecosystem dynamics in transition zones

### 4.1. Functional variables

Primary productivity is strongly related to the environmental forcing functions of temperature and moisture plus other system characteristics resulting from the environmental functions (*e.g.*, soil or-

ganic matter). Patterns of primary productivity are expected to parallel environmental gradients over regions and biomes. A null hypothesis would be that gradients in primary productivity precisely parallel gradients in climatic forcing functions.

Biomass is a product of net primary production, life history strategy, and disturbance history of the site. At one end of the spectrum, biomass approximates annual net primary productivity (*e.g.*, annual grasslands). The other extreme is represented by long-lived woody perennials for which biomass is a net accumulation of many years of net productivity. The ability to accumulate biomass is directly related to life-form and longevity, features which differ among biomes. By definition, therefore, transition zones between biomes are expected to have very steep gradients in biomass when life-forms differ. Rosen (this volume) presents an analogy between vegetation properties in transition zones and physical properties of water at temperatures of phase change. A relatively small change in temperature at 0°C results in water molecules with very different properties and different effects on other components of the system. In transition zones between different life forms, vegetation is represented by different phases and is expected to have significant effects on other system properties and processes. The mixture of properties that exist in a transition may have unique effects relative to the 'pure' states on either side of the transition (*i.e.*, analogous to water and ice). Nutrient cycling rates, resource dynamics, and resource competition all may demonstrate properties and effects out of proportion to the simple mixture of structural properties of the system. One hypothesis for nutrient cycling is that cycling rates are inversely proportional to the abundance or mass of lignin (*i.e.*, a proxy measure of vegetation structure) in the system. Thus, nutrient cycling rates should show an inverse pattern to ecosystem biomass curves in a transition zone. A different hypothesis would be that nutrient cycling rates should parallel primary production curves in a transition zone. Whether either of these hypotheses is correct or whether nutrient cycling follows a unique pattern resulting from the unique factors in transition zones has not been tested.

Climate-caused changes in distributions of plant forms are hypothesized to cause profound changes in many system properties. For example, invasion of $C_3$ perennial grasses into a $C_4$ grassland may result in many changes because of lower lignin concentrations in $C_3$ grasses as well as their cool season growing period. Predicted are decreased lignin production, increased tissue decomposition, increased mineralization of nutrients, decreased immobilization of nutrients, increased nitrification, decreased N utilization efficiency, decreased C/N ratios in soils, decreased soil moisture in spring/early summer, increased fire frequency because of increased standing dead tissue in July and August, increased herbivory, and increased belowground production. The Sevilleta LTER contains boundaries for a several $C_3$ perennial grasses, allowing tests of these predictions. Changes at the species and life-form level are expected to influence ecosystem parameters and the development of feedback mechanisms that subsequently influence species and life-form change.

## 4.2. Extrapolating field theory to biome transitions: a conceptual approach

O'Neill (1988) has suggested that we must be prepared to develop new approaches to global ecology because it is extremely difficult to measure broadscale relationships at the fine scales currently emphasized in experimental ecology. One of the relatively recent approaches that may be relevant at broad scales is ecological field theory (Wu et al. 1985; Sharpe et al. 1985, 1986; Walker et al. 1989). Ecological field theory (EFT) was originally proposed as a methodology to describe spatial interactions between individuals with overlapping zones of influence and resource competition. Definition and application of field concepts to broad scales such as the stand, region, and biome are being explored. Requirements for broad-scale methodologies highlight the limits of existing approaches, especially where they are individually based.

Environmental and resource gradients are postulated to represent the expression of higher-level fields. This is consistent with the general definition

of a field as a space over which an influence can be felt. Ideally, at the broad scale, ecological field intensity should be computed in terms of higher-level ecosystem process rates. The biome responses to higher-level environmental fields are primarily spatial and temporal changes in ecosystem process rates, including net productivity and nutrient cycling.

At the level of the individual, ecological field intensity is an integrated measure of individual stress, both as a response to the environment and to other individuals within their spheres of influence. For broad-scale applications, ecological fields provide a mechanism for spatial and temporal representation of ecosystem stress; high stress indicates high field intensity. The level of stress varies spatially along environmental gradients and temporally with seasonal or capricious fluctuations in climate. Thus, field intensity can conceptually be transformed into a broad-scale measure of integrated physiological and resource competition stress.

The definition of stress in ecology has always been a problem because it fails to distinguish between the agent of stress and the effect of stress. Grime (1979) defines the effect of stress as any reduction in optimum growth of an individual plant. Although this definition invokes the further definition of optimum growth, it has become widely accepted as a pragmatic expedient. This definition is consistent with the computation of stress in EFT applications by Sharpe et al. (1986) and Walker et al. (1989). Extending the concepts of stress and optimum performance to broader scales such as biome transition zones involves an unravelling of physiological and competitive resource interactions. Resource subsidy experiments in the form of additional water, nutrients, or both (Lauenroth and Dodd 1979; Dodd and Lauenroth 1979) show that net productivity increases may lead to invasion and replacement by plant functional groups adapted to higher resource availabilities. Carson and Barrett (1988) found that the age and physiognomy of the existing community, the type of nutrients applied, and the duration of enrichment influenced the degree to which net primary productivity was raised. Furthermore, resource subsidy in excess can lead to a different type of stress in the form of toxicity.

Defining stress and optimum performance at the biome level is even more difficult because of the wide range of adaptations to environmental gradients exhibited by the plant functional groups that compose a biome. Only as the boundaries of the biome are approached does stress become a common factor among the life-form representatives of the biome. In the transition zone, biome stress can result from either environmental or competitive constraints being exceeded. The characteristics of the biome boundary may indicate which type of constraint is operating. Where a single environmental factor such as soil moisture is determining the biome boundaries, the structural characteristics of the transition zone are likely to follow the pattern shown in Fig. 1A. On one side of the transition boundary between biome A and B, environmental constraints establish the limits of life-form B, independent of A. On the other boundary, the competitive ability of B displaces A. Alternatively, where limits are set by two different environmental constraints, such as temperature and moisture (possibly expressed as low annual or summer soil moisture, minimum temperature, or spring frost frequency), the structural characteristics of the biome boundary are more likely to diminish as the boundary is approached from either side as shown in Fig. 1B. The role of EFT at the broad scale is to provide a mechanistic spatial linkage between structural patterns of life-form dominance and functional ecosystem processes.

Climatic fluctuations interact with individual plant life-forms to generate dynamic changes in ecological field intensities, and it is the interaction of these field intensities that determines the temporal dynamics of stress for individuals. When implemented at the stand level, EFT provides the basis for describing spatial interactions between plants of different size, function, and life-form (Walker *et al.* 1989). At the biome level, the functional emphasis shifts from individual growth to constraints determining the limits of life-form representation at biome boundaries. Life-form, in turn, has a large influence on ecosystem process rates within biomes and biome transition zones.

Ecosystem processes, although they respond to many of the same stress factors, are not necessarily in phase. For example, decomposition may be highest during periods when productivity is relatively low. Applying EFT concepts at the biome level, therefore, has multiple temporal as well as spatial aspects. Higher level fields are likely to generate different ecosystem stress responses, depending upon the stage of ecosystem development and disturbance history. A quantitative definition of biome boundary stress involves some comparison with unstressed or less stressed parts of the biome. Within the geographical extent of a biome, the minimal stress or optimum condition can occur anywhere within the biome (including the transition zone), depending on the type of constraint that limits productivity. Satellite imagery using greenness indices (see later sections) may be considered as a method to identify the location of the most productive region relative to the boundary of the biome and the frequency of seasons or years when its environment approaches an optimum.

A prerequisite to applying EFT at the broad scale is a working definition of biome boundary stress. The primary characteristic of a biome boundary is a change in the vertical distribution of biomass, particularly leaf area. Secondary differences include the amount and distribution of lignin (leading to differences in rates of nutrient cycling) and rates of net primary productivity. Identification and quantification of the controlling mechanisms is a necessary first step in characterizing the broad-scale ecosystem dynamics of biome transition zones. Physiological and resource competition stress in transition zones is likely to be different from that of the biomes on either side for two reasons. First, there is a greater life-form diversity, and, second, the species in the transition zone do not represent a natural association or community. The species are in a state of tension, rather than accommodation. Under tension conditions, stress interactions among life-forms may be amplified or attenuated. Of primary interest is determining how stress interactions in tension zones affect ecosystem processes (Fig. 2A) and lead to elimination or enhancement of life-form populations at the edges of transition zones. The two edges of the transition zone are areas of instability (Fig. 2B) that may have threshold dynamics analogous to a catastrophy cusp (see next section).

Rykiel *et al.* (1988) postulate that lower-level disturbances can be amplified and propagated by ecological processes to produce significant effects at higher levels. They point out that hierarchy theory has not addressed in detail the circumstances that might lead to attenuation or amplification, although amplification had previously been considered unlikely (Allen and Starr 1982). A conceptual framework for a similar consideration of the possible modes for propagating fine-scale physiological and resource competition stresses to broad-scale interactions between biomes currently is lacking.

Transition zones represent areas where broad-scale dynamics can be observed and underlying ecosystem mechanisms controlling life-form boundaries can be unravelled. An understanding of broad-scale mechanisms for past changes in life-form composition in transition zones may provide insights for identifying factors that may be affected by global climate change. Future trends, however, will not necessarily repeat past trajectories. New interactions in the form of increasing resource abundances for carbon, increased leaf temperatures, and projected elevated increases in ambient temperatures and water use efficiencies may significantly alter biome boundary responses to soil texture and environmental stress.

### 4.3. Cusp catastrophe: a conceptual model for a transition in New Mexico

A cusp catastrophe model (Jones 1977; Jameson 1986) has interesting properties that relate to systems in semiarid environments. The model appears to fit observed phenomena relating primary production, a precipitation threshold (Sala *et al.* 1988), and the inverse texture hypothesis (Noy-Meir 1973). The inverse texture hypothesis pertains where annual precipitation fluctuates around 370 mm. Above this threshold, productivity increases with soil moisture holding capacity (SMHC), characteristic of fine-textured soils. Conversely, productivity decreases with SMHC if precipitation is below 370 mm, because coarse soils allow deeper penetration of scant moisture and reduce evaporation. A graphic illustration of the model (Fig. 3) demon-
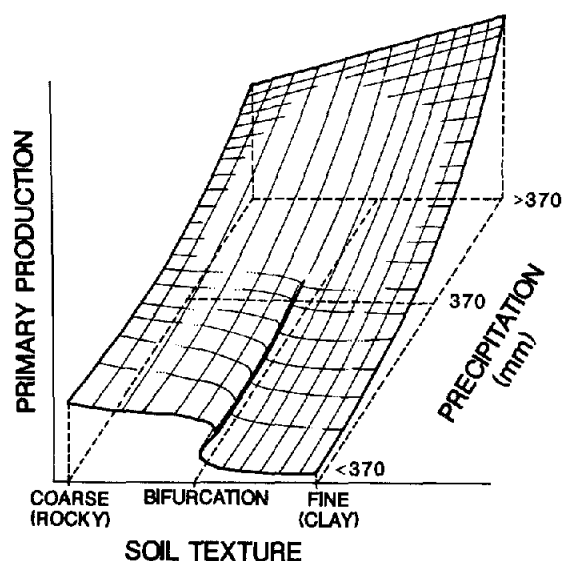


*Fig. 3.* Cusp catastrophe model for the relationship between productivity, soil texture, and precipitation. A threshold occurs at ~ 370 mm precipitation, which switches the relationship between texture and productivity (Sala *et al.* 1988). The cusp (folded edge) may reflect the dynamics of the biome transition zone in New Mexico (Sevilleta LTER).

strates the features of the cusp model. At higher precipitation quantities, there is a relatively smooth surface reflecting the gradual increase in productivity with increased SMHC (back edge in Fig. 3). For fine-textured soils (high SMHC), there is a steep, nonlinear decrease in productivity as precipitation decreases from > 370 mm to < 370 mm (right edge of figure). Coarse soils, including rocky soils, show a less steep decline in productivity with decreasing precipitation and may even demonstrate an increase at the lower precipitation levels. Very rocky soils can collect moisture in cracks, fissures, etc., and provide a combination of aeration and moisture that is more favorable than that at higher precipitation levels, where the collecting properties of the substrate reduce necessary aeration. The properties of the cusp model (Jones 1977) may be appropriate for regions having < 370 mm precipitation and intermediate textures (front edge of figure):

1. Bimodality: The system at low precipitation levels tends to be either in one biome state or another; gradients between biome types are very steep and intermediate values tend not to occur.

2. Discontinuity (catastrophe): As the controlling factor (soil texture) changes toward either extreme, a point is reached where the response can no longer move smoothly. The jump to a different level at this discontinuity is what gives catastrophe theory its name (Jameson 1986).

3. Hysteresis: The path that the response must make as the control factors move in one direction is different from the response as the control factors move in the opposite direction.

4. Divergence: This property is represented in a movement from the back edge to the front edge of the figure. A small difference in the soil texture status under moister conditions can result in development of high productivity or low productivity as the system moves toward more xeric conditions on the folded area of the figure. The area where the pathways split is called a 'bifurcation.' Bifurcations have important implications for extrapolating across scales. In passing through a bifurcation, one must understand processes on both sides of the bifurcation. Extrapolations cannot be made from the scale features represented by one set of relationships to scale features represented by a second set of relationships on the other side of the bifurcation (O'Neill, per. comm.). We hypothesize that bifurcations occur in transition zones, and, in fact, the transition may be a product of such bifurcations. In such areas, subtle changes in climate are magnified by the formation of one state (biome type) or another. Also, relatively small differences in soil texture should amplify the degree of the magnification. At the species level, different life-forms should respond to fluctuations of annual precipitations in different ways. During low precipitation years, annuals on fine-textured soils should show very low productivity relative to slightly coarser soils. Perennials integrate annual variation in precipitation and are expected to respond to decade-long patterns in precipitation or significant drought episodes. A severe drought is likely to relate to the very front edge of the cusp figure, where the fold magnitude and overlap are most pronounced. Only areas of water redistribution and collection (properties of rocky areas) of a given area have production or survival. Examples of these types have been recorded for the Sevilleta LTER in New Mexico. This conceptual model facilitates their relationships.

There are actually three states (productivity values) that could exist in the area of the fold. When climatic conditions change, this could be analogous to developing one biome type vs. another in a transition zone or to developing a third unique type. The three outcomes or solutions for a given input to such a model will make it difficult to predict the response. The multiple states of the cusp area may correspond to the conditions of amplification or attenuation hypothesized in the preceeding section. Identifying the role of interactions between species, ecosystem functions, and the role of past influences will be important research topics for verifying such models. The research program in New Mexico is addressing these topics.

## 5. Measurement techniques for broad-scale hypotheses

Environmental science has a rich history of fine-scale studies/experiments. We also are entering an era where we may be overwhelmed with remote sensing data from space. Intermediate scales at the landscape level (mesoscales, Delcourt and Delcourt 1988) may represent the weakest link in our sciences and the greatest hinderance to extrapolating to the region and globe. The following are examples of mesoscale studies which could be used to validate the conceptual approaches we have described.

### 5.1. Precipitation

The traditional precipitation gauge represents a fine-scale sampling technique, and only very long-term data sets can approximate mesoscale or broader patterns. The high variability associated with such fine-grained measurements averages out in a long-term data set, and area-based trends are revealed. In the absence of long-term data sets, gauges have varying efficiencies for capturing coarser-grained patterns. Major storm-frontal movements of moisture deliver relatively uniform precipitation quantities both in intensity and areal
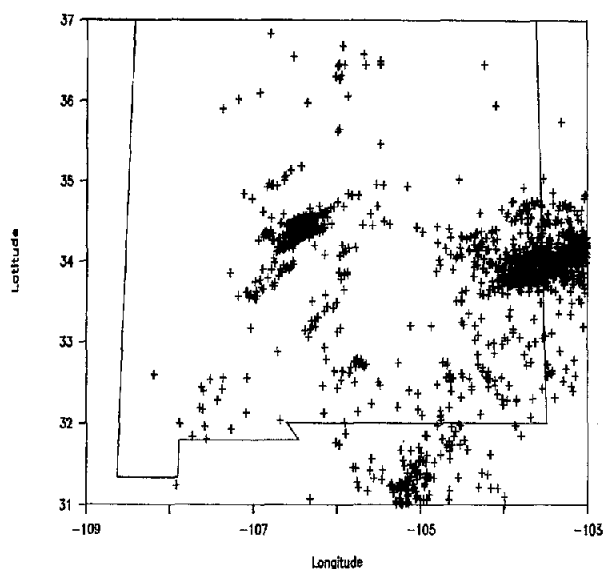
*Fig. 4.* Distribution of lightning strikes over New Mexico, USA, during September 22, 1988. The distribution of precipitation follows the same pattern for these convective thunderstorms. Patterns change daily, making this an excellent method for quantifying spatial and temporal distributions.

distribution. In areas and seasons with convective thunderstorms, the smaller, irregular, and intense distribution of precipitation is poorly sampled with a sparse network of gauges. This type of storm often yields correlation coefficients of < 0.5 for gauges several kilometers apart (Meentemeyer and Box 1987).

Summer convective storms typically are associated with lightning, which allows location and quantification of such precipitation (Fig. 4). For many years, precipitation has been thought to play a major role in separating the electric charge in thunderstorms (*e.g.*, Workman 1967) and also in initiating lightning discharges (Dawson and Duff 1970; Griffiths and Phelps 1976). It also is possible that lightning and other effects of cloud electricity enhance or otherwise affect precipitation (Szymanski *et al.* 1980). Piepgrass *et al.* (1982) summarized literature showing that average rain volume per lightning flash seems relatively independent of the geographical location of the measurement and perhaps even storm type (summer air mass vs. squall line). These results and the previous lightning-rain correlations indicate that when the me-

teorological conditions favor the production of lightning, there is almost a direct proportionality between the total rain volume and the total number of cloud-to-ground flashes (20,000 m³ of rain per lightning strike). Both minor and major storms exhibit surprisingly good correlations between lightning and rainfall when measurement of rainfall lags the lightning measurement by times of 4 and 9 minutes, respectively. If there is a cause and effect relationship between precipitation and the generation of electric charge in thunderstorms (or vice versa), then a delay in rainfall would be expected because the rain requires several minutes to fall from the 7- to 9-km altitudes of the cloud charges. Also, the precipitation associated with an electrical event may be distributed over several square kilometers by the time it reaches the ground. In the United States eleven western states have lightning location systems that can be used to map storm size, location, duration, and quantity of precipitation. In addition, other measurements can be used to validate the use of lightning location in precipitation quantification. In semiarid areas such as the Sevilleta LTER in New Mexico, precipitation events separated by a number of days cause distinguishable 'greening' of the vegetation. These phenomena can be detected by satellite remote sensing with the use of Normalized Vegetation Indices (see below). Other satellite sensors such as synthetic aperature radar (SAR) allow analysis of spatial patterns in soil moisture. The combination of precipitation gauges, lightning location, transect reflectance measurements, and remote sensing analyses can be used in a coordinated fashion to identify spatial and temporal scales associated with these evens.

## 5.2. Vegetation cover/dynamics

Traditional vegetation plots and transects identify pattern and dynamics at relatively fine scales. Often these are 1-m² to 0.1-ha plots or 1-m-wide transects. High variance in spatial pattern and temporal dynamics are common for these measurements. Numerous microscale, site-specific characteristics influence the dynamics and patterns of such measurements and make change detection or extrapola-

tion difficult. Mesoscale transects of 1- to 2-km width and 5- to 20-km length may identify the patterns associated with biome transitions; however, such transects cannot be censused feasibly with traditional approaches. In such cases complementary techniques are remote sensing from satellites, aircraft, and balloons. Recent developments in image-processing technology and geographic information systems (GIS) are important aspects of the multiple-scale and data-rich nature of these techniques.

Satellite and aircraft imagery are relatively common approaches; however, balloon platforms offer an additional scale of measurement. A hand-controlled balloon system with a gimbals-mounted camera or radiometer can be used for 1- to 100-m² plots (Gosz, unpubl.). The balloon can be rapidly walked over plots and transects, and the camera can be operated with an infrared remote control. An additional advantage is that trampling on plots is minimized. By varying the height of the balloon system, different scales can be analyzed with the same system to identify the relationship of variance with scale, within-pixel heterogeneity, and algorithms for extrapolating across scale. A single sampling system that can operate over many scales eliminates errors from different assumptions associated with different measurement systems. New camera systems utilizing still video techniques allow images to be recorded in analog form on diskettes. Diskettes can be unloaded directly into a computer and directly digitized with large savings in cost and time. Additionally, diskettes can be played in the field to assure proper coverage of plots (i.e., instant replay). The diskettes can be erased and reused.

## 5.3. Remote sensing

Remote sensing provides a means of detecting and quantifying gradients at many scales and warrants special discussion. For example, the Sevilleta LTER plans to document gradient relationships (identified by spectral pattern) within the Sevilleta and between the Sevilleta and other LTER sites (Jornada, CPER, Konza). From the many potential relationships between remotely sensed data and biophysical

parameters, two promise to be useful for most situations: visible-near infrared (vis-nIR) contrast vs. green vegetation amount and overall reflectance vs. total vegetation amount. These are identified because (1) their applicability to many vegetation types has been demonstrated, (2) green and total vegetation amounts are ecologically significant parameters, (3) the necessary satellite data are readily available on a regular basis from a variety of sources (TM, MSS, SPOT, AVHRR), and (4) instruments for near-ground measurements (i.e., hand-held radiometers) are available.

### 5.3.1. Visible-near infrared contrast vs. green vegetation

Green leaves differ from most other natural materials in having low reflectance in the visible but high reflectance in the near infrared. Vis-nIR contrast increases with the proportion of green vegetation vs. other materials in the field of view and asymptotically with the number of layers of green leaves (Gausman et al. 1976). Measures of the vis-nIR contrast (called green vegetation indices, GVIs) have been used as indices of green vegetation amount (Curran 1980). GVIs have been correlated with a wide array of measures of green and total vegetation amount, including leaf area index (Running et al. 1986), canopy cover (Foran 1987), and aboveground biomass (Huete and Jackson 1987). Relationships between GVIs and the intercepted fraction of photosynthetically active radiation and net photosynthesis have been demonstrated for homogeneous crop canopies (Hatfield et al. 1984; Sellers 1985), but their application to pixels that are complex mixtures is more difficult and is the subject of current research (Choudhury 1987).

### 5.3.2. Overall or single-band reflectance vs. total vegetation amount

The potential utility of this relationship is illustrated by the demonstrated contrasts between grazed and ungrazed land in a variety of arid and semiarid areas (Otterman 1981; Musick 1984; Ringrose and Matheson 1987). Despite the multitude of factors affecting reflectance, brightness indices have proven more useful than GVIs for estimating total
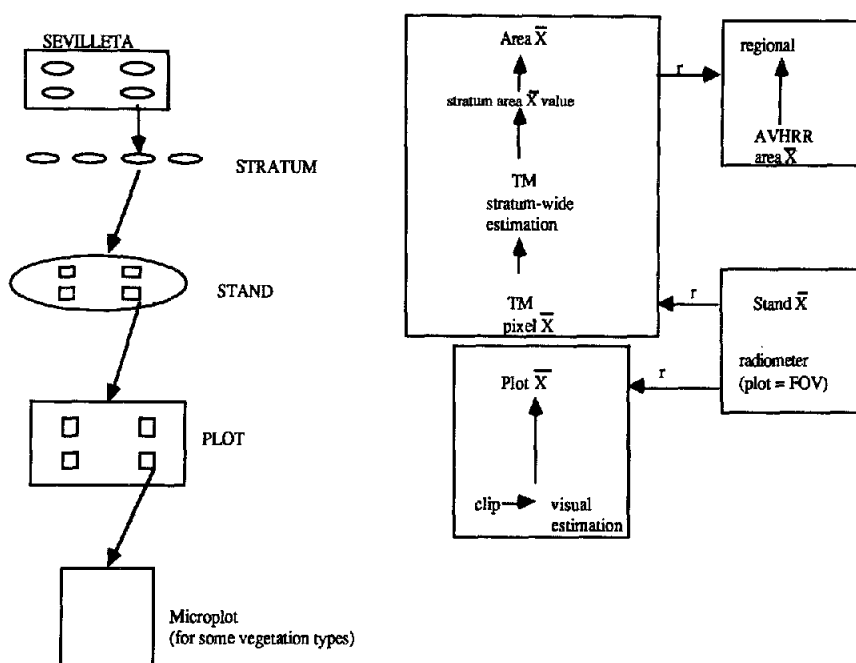
*Fig. 5.* Intercalibration of methods to translate production from standard plot studies to spectral reflectance measurements of remote sensing. The letter *r* indicates regression predictions.

canopy in arid and semiarid vegetation (Musick 1984; Ringrose and Matheson 1987). The confounding influence of soil brightness variation can be reduced by stratifying the analysis by soil type and is minimized when brightness change with time at a given location is used to indicate cover change (Musick 1984).

The gap in scale between remotely sensed data and conventional methods involves fundamental questions regarding the scale dependence of spatial and temporal variation. The number and arrangement of sample plots required to adequately measure a biophysical parameter within a pixel-size area depends on the amount and pattern of heterogeneity with the area. Because relationships between vegetation indexes and vegetation amounts are often nonlinear (Choudhury 1987), pixel-scale vegetation index values are affected by subpixel heterogeneity (Jupp *et al.* 1986; Walker *et al.* 1986). A multilevel, nested sampling design that uses near-ground reflectance and traditional vegetation measurement techniques at the plot scale can be linked with broader-area reflectance data provided by satellite-borne sensors (Fig. 5). An approach such

as this can develop a coordination of transect, quadrat, and remote data, allowing reduction of intense field methodology to a minimum without a loss of information.

### 5.4. Biotic function: biogenic gas flux

Spatial analysis of structural features in the environment is relatively easy because they can be seen by conventional approaches. Process information is less easily 'seen' and usually is inferred by relationships with analyses of structural features and change through time (*e.g.*, rate or change in primary production = change in biomass or respiration during decomposition = mass loss or gain per unit time). The dynamics of biogenic gas flux are a direct result of biological process rates; however, the standard technology for quantifying gas flux is very fine scale (*e.g.*, chamber studies, instrumented towers). New optical technologies are becoming available that directly quantify ('see') gas dynamics at coarser scales and, in addition, are not encumbered by the assumptions and constraints of
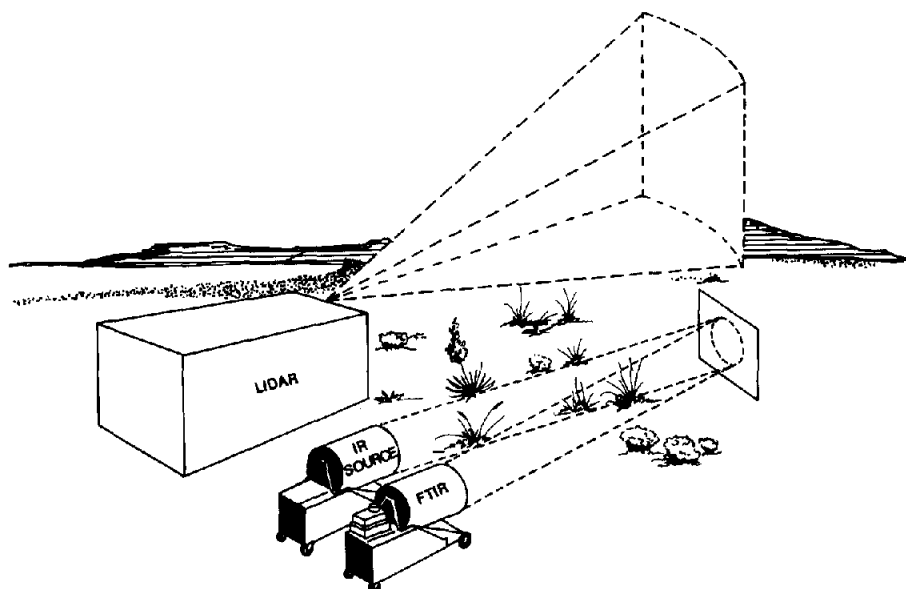
*Fig. 6.* Long-path method for quantifying gas concentrations over landscapes (Gosz *et al.* 1988). This represents a two-ended method for FTIR. Other optical techniques use UV lasers (LIDAR) which are single ended. These are examples of developing technologies for quantifying process rates over large spatial scales (kilometers).

chambers and towers. Field measurements of these trace gases can yield valuable evidence for scale dependence and heterogeneity of various biological processes where the gas flux is a proxy for biological process (Gosz *et al.* 1988).

Fourier-Transform Infrared Spectrometry (FTIR) is a promising technology for developing long-path studies of emissions of many gases simultaneously and biospheric/atmospheric interactions in natural environments (Gosz *et al.* 1988). The long-path capabilities of such instruments allow measurements that integrate the variability both spatially and temporally. Changing the path length allows studies at different scales with the same instrument, an important factor because different instruments have different assumptions or cause different artifacts. Long-path optical techniques such as FTIR are valuable because analyses can be done under field conditions without physical collection of samples and without disturbance of the conditions one is attempting to study (Fig. 6). A major challenge will be to develop methods to convert concentration measurements over a nested series of spatial scales to accurate estimates of average flux. FTIR analyses provide atmospheric gas concentra-

tion data that must be coupled with meteorological data to estimate flux. Typical micrometeorological techniques for quantifying fluxes such as eddy correlation and vertical profiling are tower-based measurements (*i.e.*, small scale). With FTIR capable of analyzing path lengths up to 1 km, single-point, detailed, site-specific meteorological measurements are not sufficient.

Another emerging technique for quantifying water vapor flux is LIght Detection And Ranging (LIDAR). This technique is being developed at Los Alamos National Laboratory, Los Alamos, New Mexico. LIDAR is a UV-laser based technique with the capability to provide a three-dimensional analysis of water vapor (and hence air-mass movement) over an area of several square kilometers. In addition to its ability to quantify evapotranspiration, coupling LIDAR with FTIR has the potential to provide a data base allowing calculation of near real-time flux of many gas molecules along the analyzed path.

These are two of the new techniques; however, many more are in the process of being developed. They will provide exceptional capabilities for analyzing at a range of scales needed for successful

extrapolations from the traditional small-scale studies to regional and global analyses. They represent the technologies necessary for testing the multiple-scale hypotheses presented for biome transitions and climatic change.

## 6. Role of networks in broad-scale studies

Transition zones can play a special role in studies of change detection and extrapolation across regions; however, networks of sites will be required to represent the large spatial scales needed to recognize and document changes that occur at those scales. The LTER program of the U.S. National Science Foundation is an example of the development of the networking capability to allow such analyses. Each site is accurately located on a continental scale so that rates of movement or the spatial scale of a particular environmental phenomena can be quantified. The development of GIS allows digitization and mapping of this information both within sites and among sites. Networking allows sites to work on a common time scale and synchronize efforts at quantifying responses to large-scale environmental phenomena. For example, an El Nino or La Nina ocean/climate event may cause very different responses among different ecological parameters at one site and among different sites. Each site has many interacting, site-specific factors; however, the initiation of the responses may well be caused by the El Nino/La Nina phenomena, a triggering effect which could be common to all sites. Such networks could identify the spatial scale of the phenomena, the times of initiation and conclusion, and the types of ecological responses that were similar and dissimilar. For some sites it could separate the triggering response from the subsequent chain of events (succession of events) until a new triggering event occurred. Some portions of regions may respond while others may not. This networking could help identify the significance of various types of constraints on systems, the regional extent of those constraints, and the sequence of ecological phenomena that is typical following changes in these constraints. That information plus the very sensitive and rapid responses expected from similar studies on transition/tension zones could improve the regional-to-global predictions that are being requested by society.

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