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VEGETATION DYNAMICS IN CHANGING ENVIRONMENTS

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Abstract

Human-induced changes in atmospheric chemistry and meteorology have the potential to alter a broad array of ecosystem processes over a range of temporal and spatial scales. These may have direct and indirect effects that could influence management strategies and landscape response to disturbances associated with natural events and land use. The extent to which forecasted global changes are effective in altering local ecosystem properties will depend upon a variety of factors. In this paper, I address species life history traits and community and landscape properties that can be used by land managers to evaluate potential manifestations of global change on a local scale.

Introduction

Conditions in the atmosphere, oceans and biosphere have followed natural cycles over the geological past. Paleo-reconstructions indicate that change is the rule, not the exception, and that the changes experienced by humans over the past several hundred years are relatively minor in relation to the kind and magnitude of change which has occurred over the past millennia. However, human activities have now become an increasingly important force driving changes in the environment. Scientific theory and evidence indicate that the extraction and utilisation of resources by rapidly expanding human populations have the potential to induce profound changes in the global environment. Intensification of industrial and land-use practices have increased concentrations of greenhouse gases and have altered surface energy flux and biophysical features in ways that potentially could produce shifts in climate and thus impact ecosystem processes. Managers of land resources must somehow accommodate the ever-increasing needs and demands of societies while mitigating pollution and threats to biodiversity and sustainability in a future environment with characteristics quite different from that of our recent experience.

Land managers are faced with several general challenges associated with resource consumption by expanding populations in the face of impending global change. These include (1) Maintenance of sustained utilisation and prevention of ecological degradation. This will be particularly critical where population pressures force intensification of agroforestry, grazing or dryland cropping onto marginal lands. Past experience suggests that recovery of degraded rangeland ecosystems may not occur over time-frames relevant to management, even with substantial cultural energy inputs. The adage "an ounce of prevention is worth a pound of cure" thus has substantial application to rangeland management. (2) Altering landscapes to increase the production of desired or needed products (as by the introduction of new species or genetically engineered varieties); and (3) restoring degraded landscapes to enhance their ecological or economic productivity and diversity. In addressing these issues of resource use in a changing climate and environment, several questions emerge:

- What will be the rate, pattern and extent of change in ecosystems? Will changes be gradual and linear or abrupt and non-linear? Will vegetation change be manifested as a re-shuffling of dominance or as radical shifts in physiognomy?
- To what extent will the distribution and productivity of key food, forage and fibre plants be affected?
- How will secondary productivity and the carrying capacity for wildlife and livestock change?

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- To what extent will plant, community and landscape sensitivity to stresses associated with resource utilisation be altered?
- How will natural disturbance regimes change under new climates and how will these changes influence vegetation processes?
- What is the prognosis for undesirable pest species and exotic invaders? What plants or animals might emerge to become new "problem" organisms; what species might emerge as "solution" organisms in land stabilisation and restoration?
- What sociopolitical and economic circumstances interact with climate to determine patterns of land use and contribute to land degradation?
- How strong are the linkages between land surface properties and atmospheric processes? How do land-use practices mitigate or accentuate climate and global change?

Predictions of future changes in the global environment are riddled with uncertainty. Changes have been and are being documented, but our understanding of their causes and our ability to predict their consequences is limited. Although ecological science has progressed significantly over the past three decades, most of the research has been at a level that is of limited use in understanding global environmental change. We are only beginning to grapple with theoretical and conceptual approaches for coupling processes that operate at different scales and for coupling interactions between landscapes, regions and continents with each other. The development of global ecosystem models has lagged behind that of global atmospheric and physical oceanographic models, largely reflecting the fact that the science of ecology is relatively young. Advances in our understanding of large-scale, long-term ecosystem processes (Schimel *et al.* 1991) will benefit ecologists and natural resource managers and provide useful inputs for coupling land surface processes to oceanic and atmospheric processes, thus improving the performance of global climate models.

Direct and indirect feedbacks which link terrestrial ecosystems with global change include interactions affecting fluxes of water, energy, nutrients, and greenhouse gases. Ojima *et al.* (1991) broadly review these interactions and discuss the importance of spatial and temporal scale in determining the strength and manifestation of land surface-atmosphere interactions. They also review core projects of the International Geosphere-Biosphere Program and the research plans proposed to develop a predictive understanding of how terrestrial ecosystems will be impacted by global change. In this paper, I review species life history traits and community and landscape properties that can be used by land managers to anticipate local manifestations of global change.

The nature of change in vegetation, soils and ecosystem processes

Human-induced changes in atmospheric chemistry and meteorology have the potential to influence a broad array of ecosystem processes over a range of spatial and temporal scales (Mooney *et al.* 1987, Schimel *et al.* 1990, 1991). Changes in temperature are expected to be accompanied by changes in cloud cover and changes in rainfall amount, seasonality, frequency and intensity (Houghton *et al.* 1992). The occurrence of extreme climatic events (frost, flooding, drought) will potentially be of more importance than changes in mean conditions, but predictions of their future frequency and magnitude are highly uncertain. Observed and expected ecosystem-level responses have been reviewed for increased atmospheric carbon dioxide (Bazzaz 1990, Mooney *et al.* 1991, Woodward *et al.* 1991), increased temperature (Emanuel *et al.* 1985a,b; Pastor and Post 1988, Melillo *et al.* 1990), acid precipitation (Schulze *et al.* 1988, Schulze 1989), nutrient deposition (Aber *et al.* 1991), tropospheric ozone (Ashmore and Bell 1991), and sulfur dioxide (Winner and Mooney 1985). The ecological consequences of atmospheric and climate change have been broadly addressed (Walker 1991, Archer 1993).

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The composition and productivity of ecosystems is expected to change in future environments, as suitable habitat for different species may move gradually and directionally or as climate-related disturbance regimes (fire, flooding, wind, pest outbreaks) change. In some cases dominance may be reapportioned among existing species or similar growth forms; in other cases radical changes in species composition and physiognomy may occur. When assessing the potential manifestation of these various and interacting components of global change with respect to a given vegetation type and the ability of biotic systems to adapt or migrate, numerous factors must be considered. Some of these are discussed in the following sections.

Species life history attributes

Differences in rates and patterns of succession result from the interaction of species with various combinations of physiological and life history traits (Huston and Smith 1987). The rate, extent and dynamics of climate-, disturbance- or management-induced shifts in vegetation would be strongly influenced by the life history characteristics of the species involved (e.g. growth rate, size, longevity, stress tolerance).

Seed production

The resource status of plants strongly influences reproductive output (Stephenson 1981, Bazzaz *et al.* 1987) and reproductive output translates into opportunities for recruitment and dispersal. Environmental changes which affect viable seed production (positively or negatively) may therefore influence species abundance in existing or new habitats. The production of dispersible, viable seed may also depend on the extent of pollinator availability and the abundance of pre- and post-dispersal seed predators in altered environments or in new geographic ranges. For species expanding their geographic ranges, seed germination, seedling establishment and development of adult plants may be possible under new climatic conditions. However, if non-climatic factors of new environments are not suitable (e.g., photoperiodic requirements for floral induction) seed production and sexual perpetuation of the population will not occur.

Seed dispersal

The extent to which species are able to migrate to new habitats that develop under future environmental conditions will depend on modes of seed dispersal and rates of climate change (Huntley 1991). Migration rates of species in response to climate changes between glacial-interglacial periods has been estimated. However, predictions of migration under future climatic conditions are very uncertain. Although the forecasted magnitude of climate change resulting from human activity is comparable to the magnitude of climate change which occurred in the late-Quaternary, the maximum rates of change differ by an order of magnitude (Schneider 1989). Plants and communities may thus be responding to a rate of climate change unprecedented in the recent geological past. Many species may not be able to disperse rapidly enough to track climate (Davis 1989). Species with slow migration rates should be identified and targeted for transplanting.

For species that produce few seeds and species that have a limited range of effective dispersal, migration would be slow relative to that of species that are adapted for long-range dispersal and/or maintain a high reproductive output. Species ill-adapted to new conditions may decrease seed production and perish from their existing range before suitable new habitats open up or before seeds can be dispersed to new habitats. Species favoured under a new climate may increase seed production and thus increase their opportunity for local recruitment and regional dispersal. Dispersal will also be influenced by the extent of habitat fragmentation. Critical thresholds of habitat connectivity may occur at spatial scales specific to the dispersal characteristics of plant populations (Gardner *et al.* 1991). Species dispersal characteristics must therefore be evaluated in the context of landscape pattern. Urban and agricultural landscapes contribute significantly to fragmentation and may constitute significant barriers to species colonisation of new habitats.

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Seed bank

Expression of the soil seed bank will interact with dispersal of new propagules to a site to influence the rate and dynamics of community change under new environmental conditions. Species with long-lived seed may persist on a site long after macroclimate changes, as long as there are periodic opportunities for seed germination and seedling establishment (see section on Biological inertia). Seeds of species presently absent or of little importance in the community may be abundant in the soil (the result of an active seed rain or a long-term accumulation) but their germination and/or establishment suppressed under the prevailing environmental conditions. Under new environmental conditions, the expression of the seedbank may change to enable rapid alterations in community composition. Seed persistence will potentially change with changing environments, perhaps increasing where climate becomes drier, and decreasing where conditions become moister.

Seedling establishment

Successful restoration efforts or changes in plant composition under new climatic regimes will require establishment of seedlings, typically the most critical phase of a plant's life-cycle. If climatic conditions change such that the dominant plants cannot successfully re-establish from seed with sufficient frequency to maintain the population, community composition is destined to change, the rate depending on longevity of plants in the present population. Our understanding of the ecophysiology and distribution of species in relation to abiotic factors is largely based on studies of adult plants. However, projections based on inferences derived from the behaviour or distribution and abundance of adult plants in relation to environmental factors may be misleading, since the scale of environmental heterogeneity that is relevant and readily studied for mature plants is of quite a different order from that which determines the fate of a seed or seedling (Harper 1977: p. 112). Establishment of new species under changed environments will also be influenced by the extent of competition from existing vegetation and rates of gap formation (resulting from death of individual plants associated with aging, stress or disturbance). In other cases, seedlings may establish but remain suppressed until disturbance or environmental change adversely affects the dominant species (Merz and Boyce 1956, Grubb 1977, Hara 1987). Where these inconspicuous "seedling reserves" exist, plant community response to climate change may be more rapid than expected. For species expanding into new ranges, successful seedling establishment may also depend on the availability of suitable species of mycorrhizae or root symbionts (E. Allen 1989, M. Allen 1989).

Vegetative reproduction

Established individuals with long life-spans may tolerate the range of climatic and atmospheric changes likely to be encountered over the upcoming decades or even centuries. Among plants capable of vegetative regeneration, ramets that succumb to stress or disturbance may be replaced vegetatively, thus perpetuating the genet. Species that endure chronically or periodically adverse conditions may thus persist long enough vegetatively to encounter infrequent windows of opportunity for successful seed production, germination and establishment. This infrequent recruitment may be sufficient to maintain the population and partially or fully compensate for mortality since the last recruitment episode and/or enable a species to increase in density by establishing in gaps left by other species. For long-lived plants, climatic episodes conducive to seedling establishment may occur more frequently than episodes which induce wide-spread mortality among adult plants. This can result in substantial vegetation inertia and create a lag in vegetation response to changing conditions.

Stress tolerance vs. competitive ability

Attributes of competitive and stress-tolerant plants have been described by Grime (1979) who proposed a classification system based on the relative importance of stress, competition and

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disturbance in determining plant life history attributes. Functional classifications may provide a useful conceptual framework for anticipating vegetation response to altered environmental conditions (Woodward and Diament 1991). For example, environmental changes which decrease resource availability or push resource modulators (e.g., temperature) to greater extremes would favour slow-growing species adapted for stress tolerance, resource conservation and resource use efficiency, whereas changes to environments characterised by greater resource availability and/or more benign temperature regimes would favour species selected for rapid growth and competitive ability (see Chapin 1980, Chapin *et al.* 1987).

Longevity

Differences in mean and maximum potential plant longevities between species will influence the frequency of gap formation and hence the propensity for community change. Other factors held equal, the rate of gap formation (= opportunities for establishment of other plant species) would be highest for short-lived species with high rates of turnover. Long-lived plants may persist for extended periods under new environmental conditions and buffer population decline under unfavourable environmental conditions, giving the illusion of community stability. Life-expectancy of the current dominants may change, depending on whether their susceptibility to density dependent and density independent mortality factors are increased or decreased under altered environmental conditions.

Genetic variability

The plasticity of individual organisms and populations to adjust to a changing environment is finite. However, species with a broad ecological amplitude and extensive genotypic or phenotypic plasticity may be more likely to persist and adjust to new environments than species which exhibit a high degree of fidelity with respect to specific environmental conditions. Changes in abundance of sensitive species may provide early warning of ecosystem change. The extent to which species might persist where present geographic ranges and future ranges predicted under new climatic conditions overlap may be determined by the degree to which specific populations have specialised with respect to present-day environmental conditions. The extent to which populations of a species are adapted to the full spectrum of conditions - including varying day length, temperature regimes, length of growing season, soils and the like - found throughout the entire range is unknown for many species. Distinct ecotypes or subspecies adapted to local conditions may not be able to survive in other parts of the species' geographic range or in new habitats where key non-climatic factors (photoperiod for example) may not be suitable for completion of the life cycle. In cases where this is true, a species may not persist or successfully migrate as predicted from assessments of moisture, temperature and nutrient requirements.

Plant community and landscape attributes

Regional physiognomy may largely reflect the prevailing macroclimate (Box 1981). However, substantial variation occurs across landscapes within a region, and broad-scale climatic variables cannot account for the spatial patterns which shape ecosystem characteristics on a local scale. As spatial and temporal frames of observation are diminished and resolution is increased, edaphic heterogeneity and disturbances (such as grazing, fire, cropping, flooding) assume greater importance in determining ecosystem structure and function. Seasonal and annual variability in weather will dictate the productivity and dynamics of populations over time. Soils, topography and elevation will influence patterns of plant distribution, growth and abundance over the landscape. These localised variations in plant distribution will subsequently influence animal distribution and abundance. The utilisation of plants by animals (grazers, browsers, granivores, etc.) will be superimposed on this background of topo-edaphic heterogeneity and climatic variability to further influence ecosystem structure and function. As a result, plant species whose adaptations to the prevailing climate and soils would make them the competitive

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dominants of the community when herbivore populations are low may assume subordinate roles or even face local extinction when certain herbivores are present.

At the community and landscape levels of organisation, changes in climatic variables that might favour certain species or growth forms or produce shifts in geographic ranges may be of little consequence if constraints imposed by soils, herbivores or recurring disturbance are not simultaneously overcome. Anticipating changes in plant distribution and abundance under new climatic regimes thus requires a working knowledge of the degree of interaction between plant, animal and environmental components.

Plants in a community vary in their physiological tolerances and will respond differently to changing environmental conditions. They will disperse, perhaps in different directions and at their own speed. As a result, communities that develop under future climatic and atmospheric conditions will not simply be displaced duplicates of those present today. New communities and new assembly rules (Keddy 1992) for species interactions will likely emerge. In some cases, there may simply be re-alignment of species distribution and abundance within historic ranges; in other cases, the geographic expansion or contraction of species ranges may alter species composition and physiognomy to form new communities without present analogs (Huntley 1991).

Succession and alternative steady states

Our ability to anticipate future changes in vegetation hinges on our understanding of processes regulating community succession, stability and resilience. How will community stability change under new climates? Stability is a measure of persistence in the face of disturbance. Two components of stability are resistance and resilience. Resistance describes the ability of the community to avoid displacement when a given type, frequency or magnitude of disturbance occurs; resilience describes the speed with which a community returns to its former state after it has been displaced from that state (Begon *et al.* 1986). We know little of these attributes or how climate change may influence them. How much environmental change can a particular community endure before significant alterations of structure and function occur? Will some communities become more resistant to change under new environmental conditions, while others become less so? Once disturbed, will the community return to its previous state? If so, how might the rate of recovery be influenced under altered environmental conditions? The concepts of resistance and resilience presume the existence of disturbance and transition thresholds. If thresholds exist, the magnitude of change a system can absorb before transitioning to an alternative state must be determined in the context of future environmental conditions. Plant and population attributes which may forecast impending changes must be quantified so that management can be adjusted to either avert undesirable shifts or to facilitate implementation of desirable shifts.

Positive and negative feedbacks

Interactions among ecosystem components are often regulated by positive or negative feedbacks which confer a degree of homeostasis. Positive feedbacks are those which reinforce deviations from a set point, while negative feedbacks halt or reverse movement away from a steady-state condition. Positive feedbacks can thus accelerate change, and negative feedbacks may enable systems to resist change.

Schlesinger *et al.* (1990) hypothesise that positive feedbacks are operational in desertification. In their proposed scenario, long-term grazing of semi-arid grasslands by livestock produces spatial and temporal heterogeneity of soil resources such as nitrogen and water. Heterogeneity of soil resources subsequently promotes establishment of desert shrubs which further localise soil resources under their canopies. As barren areas between shrubs develop, soil fertility is reduced by erosion and gaseous emissions and a greater percentage of the soil surface becomes exposed.

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Soil surface and air temperatures then increase and produce a warmer, drier micro- and mesoclimate which favours drought-tolerant shrubs over grasses. This positive feedback process is a potential mechanism by which desertification might occur in arid and semi-arid regions, independent of climate (though climatic variables would mitigate or accentuate the process).

Positive feedbacks may also be initiated by species which redirect successional processes or disturbance regimes once established. For example, woody plants such as sumac (*Rhus* spp.), honey mesquite (*Prosopis glandulosa*) and various *Acacia* spp. may facilitate the ingress and establishment of other woody species subsequent to their establishment in grasslands (Yarranton and Morrison 1974, Petranka and McPherson 1979, Hacker 1984, Yeaton and Manzanares 1986, Smith and Goodman 1987, Archer *et al.* 1988, Vitousek and Walker 1989). This facilitation may be either passive, as in providing perching structures for birds disseminating seeds of other woody species (McDonnell and Stiles 1983) or active, and associated with modification of soil and microclimate that favours establishment of other plant species. Positive feedbacks can also be initiated when the presence of species or growth forms alters disturbance regimes. This has been occurring over extensive areas of the western United States, where introduced annual brome grasses (*Bromus* spp.) have increased the frequency and areal extent of fire in a self-reinforcing fashion to cause conversion of perennial sagebrush (*Artemisia* spp.)-steppe to annual grassland (McArthur *et al.* 1990).

The rate and magnitude of future changes in community structure and function may thus depend on the degree to which new combinations of species influence positive and negative feedbacks within the community and hence dictate future trajectories of plant succession. Resource managers can potentially manipulate organisms and ecosystem processes to (1) reinforce negative feedbacks or negate positive feedbacks to enhance stability; or (2) augment positive feedbacks to facilitate desired change.

Species diversity

Growth of each species in a community is limited by a different combination of environmental factors. Fluctuation in weather causes production of individual species to vary substantially from year to year. However, production of the whole community may be more stable, because years favourable for growth of some species cause a compensatory decrease in growth of other species (Chapin *et al.* 1987). Conversely, in stressful years the loss of productivity of some species may be compensated for by growth of others. As a result, changes in relative growth rates and abundances of co-occurring species tend to stabilise ecosystem processes such as primary production. Patterns of species rearrangement and community productivity under future environments may therefore be a function of the available species pool. Species availability, in turn, will be influenced to a large extent by changes in local and regional biodiversity associated with anthropogenic resource utilisation.

Biological inertia

The extent to which shifts in vegetation structure lag behind the climatic changes which drive them, and the extent to which vegetation can ever be said to be in equilibrium with climate are not easily determined (Davis 1989, Cole 1985, Lewin 1985). Some organisms track climate closely, reacting to conditions each year, while others respond so slowly that only long-term climatic trends have any observable impact (Davis 1984). As described in the previous section, vegetation established from seed under one climatic regime may persist under an altered regime in a vegetative state or by maintaining a persistent seed bank and exploiting infrequent windows of opportunity for seedling establishment. Modern vegetation-climate correlations which form the basis for projection of new vegetation states under future climatic regimes may be spurious or low in cases where vegetation inertia is high. Biological inertia also accounts for the considerable difficulty in management attempts to displace undesirable vegetation, even with substantial inputs of herbicides, seed, etc. Depending on the direction and magnitude of climate and atmospheric change, vegetation resistance may be relaxed or fortified.

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Anthropogenic and climate-related disturbances could reduce vegetation inertia by short-circuiting the slower process of gap-initiation and species overturn associated with old-age mortality. Frequency of disturbance may be increased under future climates as a result of weather patterns more likely to cause fire (Torn and Fried 1992), windthrow and flooding. Higher rates of disturbance would increase the rate of gap formation and chances for establishment of new plants better adapted to modified climatic conditions (Overpeck *et al.* 1990)

Boundary dynamics

Boundaries between plant communities or plant formations represent likely sites for species retreat or advancement, and global change is likely to affect the location, shape and composition of landscape boundaries. Species near the extremes of their geographic ranges and ecotonal zones between plant communities and biomes will likely be most sensitive and responsive to climate change or changes in disturbance regimes related to climate (Hansen *et al.* 1988). The distribution of plant life forms is closely coupled to macroclimate and natural plant "life form ecotones" cover 30% of earth's land surface (Box 1981). As a result, the potential for change is great. However, patterns of change will likely not be uniform and will depend upon the extent to which landscapes are fragmented, rates of habitat displacement, and species extinction and migration rates. Turner *et al.* (1991) illustrate how these factors can be evaluated for specific species and sites to identify the combinations of parameters which allow successful colonisation and those for which community survival is jeopardised. Moody and Mack (1988) found the spread of invading plants to be primarily regulated by the dynamics of satellite stands rather than expansion of initially large stands. This suggests that management efforts aimed at containing undesirable species or facilitating the spread of desirable species should be focused on outlying patches rather than large, intact stands.

Edaphic properties

Soil is the largest terrestrial pool of carbon, nitrogen and sulphur and is intimately involved in the fluxes of these important greenhouse elements between land and atmosphere. Changes in management and climate have substantial potential to influence the extent to which soils are sources or sinks for key atmospheric gases (e.g. Mosier *et al.* 1991, Ojima *et al.* 1992). Soil organic carbon (SOC) may be the single best indicator of ecosystem status in grassland and agricultural systems, both as an integrator of long-term productivity and decomposition and as an index of soil fertility (Burke *et al.* 1989). Results of a regional analysis of the North American Great Plains grasslands predict reductions in SOC storage under carbon dioxide-altered climates, the result of increased decomposition rates associated with increased temperatures (Burke *et al.* 1991). Losses were greatest in areas with high precipitation and high initial SOC; sandy soils had smaller absolute SOC losses than fine-textured soils, but higher losses relative to the total. Slight (<10%) increases in aboveground net primary production (ANPP) were predicted over the 50-year simulation. However, losses of SOC to the atmosphere were small relative to historical cultivation effects, illustrating the importance of land management on regional carbon balance and soil properties. Preservation of soil integrity is a key issue for both present and future environments, especially where climatic changes may lead to increased vulnerability to wind and water erosion (e.g., by effecting decreased plant cover, increased rainfall intensity).

Except in cases of recent land degradation and erosion, present-day soils largely reflect characteristics developed over the past centuries and their ability to support an alternative vegetation that might otherwise be well-adapted to future climatic regimes may be limited. Changes in topographic features potentially required to support new vegetation types could lag far behind changes in climate and would be constrained by parent material and geomorphology. In other cases, soil properties related to nutrient availability (associated with altered pH and mineralisation [Schimel *et al.* 1990], nutrient deposition [Aber *et al.* 1991]) or salinity (Western and van Praet 1973) may change rapidly in response to global change, and markedly influence

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species or growth form composition and productivity and plant community response to climate change (e.g. Pastor and Post 1988). See Swift (1991) for proposed IGBP research agenda on soil fertility and global change.

Potential versus realised change

The following are additional considerations for evaluating the extent to which potential changes in ecosystem structure and function associated with changes in atmospheric physiochemical processes might be realised.

Seasonality, means and extremes

When environmental change is relatively gradual or when there are shifts in seasonality, productivity of existing species may be differentially affected, producing short-term changes in patterns of growth, biomass distribution, seed production, and susceptibility to stress. Shifts in the direction and intensity of competitive interactions, plant longevity and recruitment would eventually produce changes in composition. Over the short-term, it will be difficult to distinguish fluctuation associated with climatic variability from directional change.

For a species to persist in a community, it must be adapted to the range of conditions likely to be experienced over its life cycle. Infrequent but recurring events such as drought, flooding, extreme temperatures, high winds, and herbivore or pathogen outbreaks may therefore limit the occurrence of organisms otherwise well-suited to mean conditions. Conversely, opportunities for seedling establishment may be infrequent and triggered by infrequent combinations of events (e.g. Beatley, 1974, Griffin and Friedel 1985, Turner 1990). Where infrequent events exert strong and long-lasting influences, correlations of ecosystem processes with mean or seasonal attributes may be low or misleading and patterns of change will be abrupt and non-linear. As a result, changes in the frequency, magnitude and timing of extreme climatic events may be a more important determinant of ecosystem dynamics and structure than shifts in mean values (Katz and Brown 1992).

Interactions and necessary/sufficient conditions

It is necessary for some conditions to change if ecosystems are to change. However, because of thresholds, inertia, limiting factors and interactions, a change in one or more conditions does not necessarily mean that a change in ecosystem status will follow. Thus, certain kinds of changes may be necessary, but by themselves are not sufficient to alter structure and function.

The influence of changing a certain variable(s) on ecosystem structure will be determined by the magnitude, direction and duration of the change and the extent to which the change is either augmented (positive feedback, synergism) or negated (negative feedback) by other variables. As a result, a carbon dioxide fertiliser effect, which has the potential to increase productivity and shift composition from C4 to C3 species, may not be realised unless constraints imposed by moisture and nitrogen availability are simultaneously overcome. Changes in ANPP under new climates may not translate as expected into increased secondary productivity if plant allocation to secondary chemicals or structural compounds is altered to affect digestibility. Climatic changes favouring the replacement of grasses by trees and shrubs may not be realised if seed predators and browsers that utilise woody vegetation are present or if fire regimes are maintained or are increased. Conversely, selective grazing by wildlife or livestock may elicit a shift from grassland to shrubland quite independent of climate. Increased precipitation has the potential to induce shifts in production and species composition, but if this is accompanied by reductions in photosynthetically active radiation (associated with increased cloudiness) or increases in salinity (associated with elevation of water tables), the type of change will be quite different from that predicted from rainfall alone. These examples reflect the fact that system behaviour predicted from the evaluation of individual components will often be quite different from the behaviour manifested when multiple components are interacting.

Conclusions

Ecological science has progressed significantly over the past three decades, but most of the research has been at a level that is of limited use in understanding global environmental processes sufficiently well that changes can be predicted. Descriptive studies have documented change, but often do not reveal causes or mechanisms. Empirical, experimental studies that require the scientific rigour of manipulation and replication are typically small-scale, occur over brief time periods and are focused on a few variables. While such approaches quantify relationships, processes and mechanisms, their relevance in the context of processes operating at greater spatial and temporal scales remains uncertain. Two major kinds of research have been advocated to develop the intellectual and technological tools needed to tackle issues of global change (Brown and Roughgarden 1989): (1) theoretical and empirical studies of the phenomenon of scale and the coupling of processes operating at different scales; and (2) field and modelling studies explicitly incorporating the diverse effects of humans on ecosystems and ecological processes.

Until the specifics of climate change become apparent, we cannot make any firm predictions about their effects on rangelands. Recent reviews of climate-carbon dioxide interactions in the context of grassland responses to global change (Hall and Scurlock 1991; Long and Hutchinson 1991) conclude there is insufficient information to predict accurately the response of primary production to climate change and carbon dioxide enrichment. Species, growth forms and life forms are likely to vary in their response to elevated carbon dioxide. Field and modelling experiments indicate that climatic influences on nutrient availability and water stress affect response to elevated carbon dioxide and that ecosystems vary in the extent to which these factors control function. Feedback effects through environmental variables such as temperature, water and nutrient stress may be at least as significant as the increase in atmospheric carbon dioxide, but there is scarcely enough data present to develop and validate modelling. The potential complexity of responses calls for direct experimentation on systems with diverse characteristics at scales where feedbacks between biotic systems and atmospheric properties can be manipulated and quantified to parameterise simulation models (Mooney *et al.* 1991).

At the local level, natural resource managers should use their knowledge of climatic influences and plant life-history attributes, disturbance impacts and successional processes to anticipate future change and to identify circumstances whereby desirable transitions can be augmented or facilitated and undesirable transitions mitigated or avoided. In systems where climatic variability is the rule rather than the exception, situations conducive to vegetation improvement or deterioration may arise infrequently and unexpectedly. Failure to recognise and respond to either situation constitutes missed opportunity. If the potential for transition to undesirable states is ignored, long-lasting, potentially irreversible impacts can result. Conversely, progressive and flexible management schemes which can capitalise on infrequent windows of opportunity for vegetation improvement may realise long-term benefits.

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