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Assessing and Interpreting Grass–Woody Plant Dynamics

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INTRODUCTION

In many arid and semiarid systems, grazing by domestic herbivores is a primary land use for commercial enterprises, pastoral societies and subsistence cultures. Ecosystem sustainability for livestock production requires management which maintains the soil resource and ensures a favourable balance between palatable and unpalatable vegetation. In many arid and semiarid systems, this means: (i) regulating grazing to maintain cover and production of palatable, perennial grasses that are the forage base for livestock or wildlife; and (ii) limiting invasion or encroachment by unpalatable woody vegetation. Improper management may contribute to detrimental changes that ultimately reduce both plant and animal productivity and diversity, increase the need for expensive supplemental feeding, increase the potential for soil erosion and increase the probability that expensive rehabilitation practices will be required to stabilize or restore sites. On a global scale, grazing-induced alterations of plant cover and soil processes may constitute important feedback to climate and atmospheric chemistry (Schlesinger *et al.*, 1990). General effects of grazing on energy flow and nutrient cycling (Detling, 1988), biodiversity (McNaughton, 1993, 1994; West, 1993), vegetation composition and soil properties (Archer and Smeins, 1991; Thurow, 1991; Skarpe, 1991; Milchunas and Lauenroth, 1993; Milton *et al.*, 1994, Pieper, 1994) and successional dynamics (Westoby *et al.*, 1989; Friedel, 1991; Stafford Smith and Pickup, 1993) have been recently reviewed. Other chapters in this book focus on responses of herbaceous vegetation to grazing. This chapter examines woody plant–grass dynamics and reviews approaches for enhancing our understanding of the rates, dynamics and causes of increased abundance of unpalatable woody vegetation on grazed landscapes.

Displacement of grasses by woody plants over the past century has been widely reported for arid and semiarid rangelands (see Table 1 in Archer, 1995a). Even so, our knowledge of the rates, dynamics, patterns and extent of this phenomenon is limited. Available data indicate these directional shifts in life-form abundance have been: (i) rapid, with substantial changes occurring over 50- to 100-year time spans; (ii) non-linear and accentuated by episodic climatic events (drought or above-normal rainfall); (iii) locally influenced by topoedaphic factors; and (iv) non-reversible over time-frames relevant to management.

Explanations for historical increases in abundance of woody plants in dryland ecosystems centre around changes in climatic, grazing and fire regimes and atmospheric carbon dioxide (CO_2) enrichment (see Archer, 1994; Miller and Wigand, 1994; Archer *et al.*, 1995). Influences of domestic and native herbivores on the balance between grasses and woody plants have been specifically addressed, with emphasis on the critical seedling establishment phase of the woody plant life cycle (Archer, 1995b). However, broad-scale understanding of grass–woody plant dynamics is limited by a paucity of spatially explicit information at the landscape level of resolution. Spatial heterogeneity and temporal variability in rangelands impose significant constraints on our ability to inventory, monitor, predict and manage vegetation and soils at scales of time (decades) and space (hundreds of hectares) relevant to management (Stafford Smith and Pickup, 1993; M. Stafford Smith, Chapter 12, this volume). Here, I briefly review approaches for interpreting vegetation dynamics of grazed systems across hierarchical scales of time and space with an emphasis on woody plants. I then focus on the application of an array of underutilized tools that can be used alone or in concert to: (i) further our quantitative and conceptual understanding of spatial and temporal heterogeneity; (ii) develop comprehensive monitoring schemes; (iii) evaluate land management impacts on vegetation; and (iv) temper expectations with regard to range improvement practices and rehabilitation efforts.

LIVESTOCK AND WILDLIFE

Although livestock are typically the focus of attention in managed systems, activities of native or feral herbivores, both above and below ground, should not be overlooked. In many rangeland settings, managers have little information about or control over the population dynamics of these animals. When proportions of browsers or grazers shift in response to environmental change or management, the balance between grasses and woody plants shifts accordingly (Sinclair, 1979). In some cases, management for livestock enhances the abundance of native grazers, thus putting additional pressure on vegetation and soils. Activities of inconspicuous nocturnal granivores (Brown and Heske, 1990) or consumption of plant roots by nematodes (Coleman *et al.*, 1976) or grubs (Lura and Nyren, 1992) may have a comparable to greater effect on vegetation than livestock. The influence of insects, arthropods, rodents and soil invertebrates on vegetation dynamics relative to that of the more conspicuous large herbivores is seldom known. Activities of these organisms not accounted for in field studies may obscure our understanding of livestock grazing effects on plant community dynamics, thus making it difficult to compare studies meaningfully.

DEFOLIATION OF GRASSES VERSUS GRAZING ON LANDSCAPES

Plant species composition and productivity within a region are largely a function of the prevailing climate. However, substantial variation occurs across landscapes, and broad-scale climatic factors cannot account for the spatial patterns which shape vegetation form and function at a local scale. Soils and topography exert a strong influence on patterns of plant distribution, growth and abundance through regulation of water and nutrient availability. Grazing influences are superimposed on this background of topoedaphic heterogeneity and climatic variability to further influence vegetation structure and ecosystem processes. Species adapted to the prevailing climate and soils might be the competitive dominants of the community under conditions of minimal grazing, but may assume subordinate roles or even face local extinction as grazing intensity increases.

At community and landscape levels of resolution, grazing influences on ecosystem processes and plant community dynamics are both direct and indirect, and vary across the landscape depending on the type of grazing animal, seasonal patterns of animal distribution, soils, topography and distance from resources such as water or shade. Direct effects of herbivores are those associated with the consumption or trampling of plant tissues and subsequent changes in growth, biomass allocation and vegetative and sexual reproduction. The role of herbivores as agents of seed dispersal (Janzen, 1984; Brown and Archer, 1987) and predation (Brown and Heske, 1990) is also potentially important in regulating plant population dynamics. Indirect effects of grazing include alteration of microenvironment, changes in soil physical and chemical properties, hydrology and erosion, disruption of algal or lichen crusts and the redistribution and transformation of nutrients across the landscape (Thurow, 1991; Williams and Chartres, 1991; Ludwig and Tongway, 1993). These, in turn, may feed back to affect plant growth, reproduction and seedling establishment and intensify defoliation impacts. Alterations in plant density and cover by grazers can intensify run-off/run-on patterns across the landscape and accentuate natural heterogeneity. Systems where soil resources are plant-controlled rather than terrain-controlled may be particularly sensitive to grazing (Ludwig *et al.*, 1994; Tongway and Ludwig, 1994). Alterations of microclimate, local hydrology and nutrients by grazing may favour unpalatable, nitrogen (N_2)-fixing woody plants (e.g. *Prosopis*, *Acacia* spp.) and evergreen growth forms tolerant of low nutrient conditions and water stress.

Preferential utilization of plants which vary in their palatability or sensitivity to defoliation can directionally alter the nature and intensity of plant competitive interactions and influence population dynamics and hence species composition (see Chapters 2 and 3 by D.D. Briske and J.J. Bullock respectively, this volume). Alterations in species composition and productivity combine to influence soil physical properties, nutrient cycling and microclimate. Species effects on nutrient cycling can be as important as or more important than abiotic factors in controlling ecosystem fertility (Hobbie, 1992). Changes in species composition associated with selective grazing typically result in replacement of palatable plants by unpalatable plants and reductions in litter quality. This reflects the fact that plants which produce easily decomposable litter are also those which will be heavily grazed, because the same chemical properties that determine litter decay also determine palatability and digestibility (Pastor and Naiman, 1992). Changes in amount and quality of litter associated with changes in species composition can lead to reductions in microbial biomass, mineralization and respiration. Plants which remain or increase with grazing may further reduce rates of nutrient cycling, thus accentuating defoliation stress and influencing species composition, plant cover and production. Changes in soil nutrient distribution subsequent to establishment of woody plants may feed back to increase the likelihood of additional woody plant encroachment, increase the spatial heterogeneity of nutrient distribution and accelerate water and wind erosion (Schlesinger *et al.*, 1990). The rate and direction of succession following relaxation of grazing may largely depend on the degree to which soil properties and processes have been affected. Unfortunately, there are no clear generalizations which emerge with respect to grazing impacts on soils (Milchunas and Lauenroth, 1993). This may reflect the fact that most studies have been initiated only after sites have already experienced varying and unknown degrees of historical grazing.

Plant distributions and patch structure vary along environmental gradients within pastures and management units. The likelihood of being grazed by a specific class of herbivore and the plants' response to grazing vary along these gradients, depending on water and nutrient availability and neighbourhood effects. Fluctuation in rainfall may accentuate or mitigate grazing impacts on vegetation. Grass consumption also reduces the amount and continuity of fine fuels and hence the frequency, pattern and areal extent of fire (Wright and Bailey, 1982; Savage and Swetnam, 1990). As a result, successful management of the balance between grasses and woody vegetation requires a spatially explicit understanding of the interactive roles of climate, soils, topography, fire and herbivory over time (Fig. 4.1). Given the complexity of interactions among soil properties, resource availability and climatic stresses on plant growth and survival, it can be difficult to ascribe adaptive significance to traits that enable plants to tolerate or evade herbivory. For example, some graminoid traits which may have originally evolved in response to selection pressures imposed by water stress, fire or

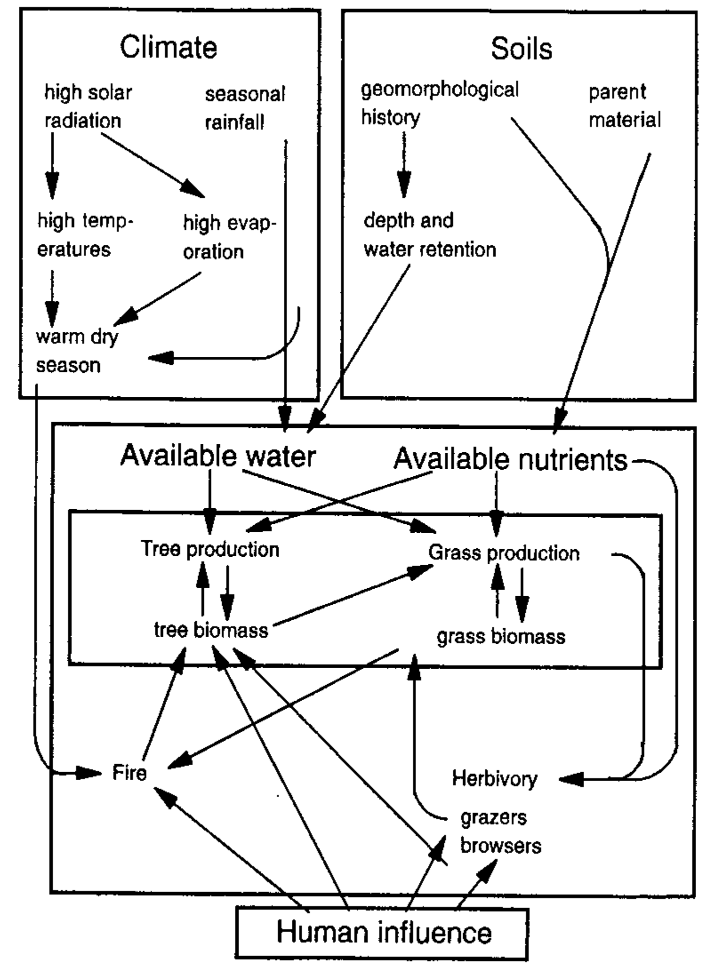

Fig. 4.1. Understanding and interpreting changes in grass–woody plant abundance requires a spatially explicit knowledge of interacting biotic and abiotic factors (from Scholes and Walker, 1993).

competition also confer benefits to grazed plants (Coughenour, 1985). As a result, screening of plant genotypes or the placement of species into 'functional groups' with respect to grazing requires evaluation of responses to multiple stresses and broad sets of interacting parameters.

To understand fully the influence of grazing impacts on ecosystem dynamics, it is essential to identify levels in a hierarchy of landscape organization, the key processes that occur at each level, interrelationships among levels, and interactive influences of other disturbance or environmental factors (Archer and Tieszen, 1986). Modification of microclimate, plant competitive interactions, soil processes and fire frequency associated with the defoliation and preferential utilization of grasses can benefit unpalatable woody plants in several ways. These include increased probabilities of successful seedling establishment, greater growth rates, decreased time to reproductive maturity, increased frequency and magnitude of seed production and extended longevity (Archer, 1995b, and references therein).

STATES AND TRANSITIONS

Management and conservation of grazed rangelands depends on knowledge of likely vegetation states and the transitions affecting those states (Fig. 4.2). In many arid and semiarid regions, the 'state and transition' model (Westoby *et al.*, 1989) provides a more suitable conceptual framework for interpreting vegetation dynamics than the traditional equilibrium-based successional models. Vegetation 'states' are recognizable and relatively stable assemblages of species occupying a site; transitions between states are triggered either by natural events or by management actions. This approach is flexible, incorporates cyclic and successional processes and stochastic responses of vegetation to climate or biotic disturbance.

Applications of this concept relative to equilibrium-based models have been widely reviewed (Archer, 1989; Friedel, 1991; Laycock, 1991; Ellis, 1992; Dankwerts *et al.*, 1993; Joyce, 1993; Walker, 1993; Borman and Pyke, 1994; Whalley, 1994; M. Stafford Smith, Chapter 12, this volume). Specific examples from different rangeland systems are accumulating (George *et al.*, 1992; Huntsinger and Bartolome, 1992; Jones, 1992; Milton *et al.*, 1994; special issue of *Tropical Grasslands* 28(4), 1994). While the state and transition approach is valuable for management and classification, the definition of states is largely heuristic and proposed mechanisms for transitions between states are often hypothetical rather than empirical. Studies quantifying rates and probabilities of transition among states are uncommon. Similarly, the role of 'triggering' events which might initiate or drive transitions are not well understood. As a result, it is difficult to predict the longevity of a given vegetation state and the level (frequency, intensity, duration) of stress, disturbance or environmental change required to shift vegetation from one state to another. Generalizations regarding the rate or extent to which 'recovery' to a previous state occurs after disturbance or following relaxation of grazing are equally elusive. Transitions will depend on complex interactions between species life-history attributes, availability of propagule sources, the extent to which soils have changed, and climatic conditions.

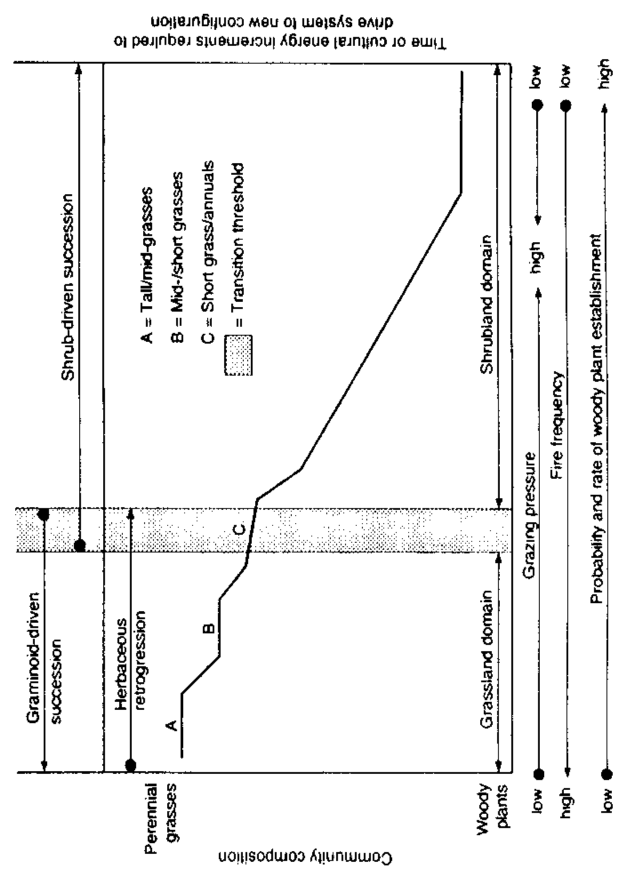

Fig. 4.2. Conceptual model of grass and woody plant abundance in grazed ecosystems, postulating the existence of a threshold of disturbance (grazing-driven) in triggering a successional transition between vegetation states dominated by grasses and woody plants (from Archer, 1989). The threshold of herbaceous utilization required to enable some woody species to successfully establish from seed can be readily exceeded, even at low levels of grazing in some systems (Archer, 1995b).

Thresholds

The conceptual model in Fig. 4.2 illustrates how grazing animals can direct plant succession to effect changes in vegetation structure. This model is predicated on the existence of transition thresholds, the evidence of which is based on widespread observations of abrupt, non-linear changes in vegetation composition in arid and semiarid systems (Buffington and Herbel, 1965; Herbel *et al.*, 1972; Archer *et al.*, 1988; Friedel, 1991). These thresholds may exist for various herbaceous transitions (perennial ↔ annual; tallgrass ↔ shortgrass), for transitions among woody elements (palatable ↔ unpalatable; suffruticose ↔ fruticose ↔ arborescent; deciduous ↔ evergreen) and for herbaceous ↔ woody transitions.

Vegetation within a particular state or 'domain' may be relatively stable and resistant to change. Intensification of grazing will alter herbaceous composition as animals preferentially utilize certain species, some of which may be relatively intolerant of defoliation (Briske, Chapter 2, this volume). These species are replaced by less preferred or more grazing-tolerant species. Gaps formed by mortality of grazed plants or a decline in their canopy or basal area represent opportunities for establishment of other species. As a result, diversity may increase (Milchunas *et al.*, 1988). If grazing pressure is relaxed prior to some critical threshold, succession may return the site to its earlier composition, the rate of recovery being influenced by climatic conditions and the extent to which soil structure and fertility may have changed. If grazing intensity is maintained, herbaceous biomass (above and below ground) may decline and the capacity of grazed plants to competitively exclude other plants will diminish. Increases in size and density of unpalatable plants, woody or herbaceous, will further intensify grazing pressure on remaining palatable herbaceous plants. As woody plants establish, new successional processes and positive (self-reinforcing) feedbacks drive the system to a new state (e.g. Archer *et al.*, 1988; Schlesinger *et al.*, 1990). The woody plant seed bank may increase and established trees and shrubs often have high vegetative regenerative potentials and extended longevities (decades to centuries). Reductions in palatable grass seed production and a deterioration of their seed bank make a return to grass domination unlikely, even when livestock are removed. Stochastic climatic events (drought, frost) may hasten grazing-mediated transitions (e.g. O'Connor, 1993, 1994). Transitions may be accelerated if keystone plant species establish and initiate strong positive feedbacks which drive successional processes or change disturbance regimes. For example, *Prosopis glandulosa*, an invasive shrub of grasslands and savannas of southwestern North America, alters soils and microclimate subsequent to its establishment in grass stands and facilitates the dispersal and establishment of additional woody species (Archer, 1995a). Introduced annual *Bromus* spp. readily invade grazed shrub steppe in North American cold deserts and have increased the frequency and areal extent of fire in a self-reinforcing fashion to trigger conversion to annual grasslands over extensive areas (Billings, 1994).

Little is known of the nature of transition thresholds or how to anticipate when we might be approaching one so that management can be adjusted to avert undesirable change. Multivariate analyses have been used to reduce complex species composition data into a few functional groups (Friedel *et al.*, 1988; Bosch and Booysen, 1992). The potential therefore exists to characterize the configuration of communities that exist on either side of a threshold in terms of the relative proportions of a few groups, under specified seasonal conditions (Friedel, 1991). Identification of demographic variables (size class distribution, critical minimum basal area, tiller and plant density, seed production) that portend thresholds between states might yield a mechanistic basis for monitoring to anticipate change (see chapters 2 and 3).

Figure 4.2 proposes a critical grazing threshold beyond which the probability of woody plant recruitment increases markedly. In many cases, the threshold of herbaceous utilization required to enable woody plants to establish from seed appears to be readily exceeded, even at low levels of grazing (Archer, 1995b). Increases in grass biomass, achieved experimentally or by relaxing grazing, can slow rates of woody plant seedling establishment and growth, but may not prevent it. For example, savannas of the Edwards Plateau of central Texas have been heavily and continuously grazed since the mid-1800s. In 1948, several grazing systems were implemented on an experimental station in this region. Cover of unpalatable evergreen shrubs has increased two- to fourfold since 1948, despite the relaxation or exclusion of livestock grazing (Table 4.1). Ironically, the greatest increases were on pastures protected from livestock grazing. Such data suggest that, by the time progressive grazing management practices were implemented in 1948, these systems were already in the woody plant 'domain of attraction' (Fig. 4.2); changes in soils, microclimate, seed bank and vegetative regeneration potential were such that succession toward woodland was under way and perhaps inevitable. In cases such as these, grazing management schemes may have to aggressively incorporate the use of fire. Proper grass utilization and maintenance of herbaceous composition alone may not be sufficient to successfully curtail woody plant encroachment.

Table 4.1. Woody species composition (% of total canopy cover) and total canopy cover for three pastures in 1949 and 1983. All areas had been continuously and heavily grazed since the mid-1800s, until establishment of the pastures in 1948. Pastures were grazed by cattle, sheep and goats (60–20–20 ratios); exclosure was protected from livestock grazing but not wildlife. (From Smeins and Merrill, 1988.)

	Continuous		Rotation		Exclosure	
Species	1949	1983	1949	1983	1949	1983
Quercus spp.	89	41	90	50	93	41
Juniperus spp.	7	40	4	39	3	32
Other species	4	19	6	11	4	27
Total canopy cover	14	10	10	30	8	35

Woody plant encroachment is a subtle process that operates at decadal time-scales. Forces setting the process of invasion in motion may occur long before results are readily apparent. By the time results are manifested, cost-effective management options may have been precluded. Communities and landscapes may have a gross, outward appearance of stability for many years and then change radically over a short period of time. In some systems this reflects the importance of rare or infrequent events which trigger episodes of seed production, seed dispersal or seedling establishment. It can also reflect patterns of plant growth and development, whereby 'seedlings' persist, inconspicuously distributed throughout the herbaceous vegetation (Archer, 1995b). After several years, there is a dramatic shift in allocation to shoot growth. Such plants may not be apparent to the casual observer until many years after their establishment, by which time they are highly persistent members of the plant community. Given these patterns of growth, it is important to closely monitor rangelands where bush encroachment is a potential problem.

Vegetation change following relaxation of grazing

Changes in rangeland vegetation tend to be slow in dry environments and observational time scales that exceed a human lifespan are required to separate directional trends from fluctuations associated with weather-driven variability (Collins *et al.*, 1987). Long-term data sets from Utah indicate that recovery of palatable shrubs and perennial grasses (three- to tenfold increase in canopy cover) has occurred since 1933, following implementation of federal legislation which led to reductions in livestock grazing (Yorks *et al.*, 1992, 1994). Similarly, differences in albedo, soil temperature, soil moisture retention and vegetation 'greenness' along the USA–Mexico border appear related to relaxation of grazing pressure in the USA since passage of the Taylor Grazing Act in 1934 (Bryant *et al.*, 1990). However, widespread observations indicate that, once critical thresholds are crossed, grazing-induced changes in composition of arid and semi-arid rangelands will not be reversed simply by removal of livestock, especially where palatable plants are rare and unpalatable perennials predominate (see Archer, 1989; Westoby *et al.*, 1989; Archer and Smeins, 1991; Walker, 1993). This may reflect differences in seed production among grazed, palatable plants (low, infrequent) and less grazed, unpalatable species (high, frequent), competitive suppression of seedlings of palatable species by high densities of established, long-lived unpalatable species, lack of suitable microsites for establishment of palatable species (variable microclimate, soil compaction, reduced infiltration, loss of microsymbionts), and loss of species involved in keystone processes related to soil nutrient availability, pollination, dispersal, or mediation of competitive interactions (e.g. Bond, 1993).

Reversal of transitions may require active intervention by land managers and may involve clearing of bush (mechanical, chemical), fertilizing and seeding. All

are costly, are risky in terms of the probability of achieving goals and have the potential to exacerbate existing problems. In many cases, unpalatable plants are not a problem *per se*. Rather, they may be symptomatic of past management transgressions (McKell, 1989). While vegetation dominated by unpalatable perennials may not be desirable, such plants reflect the prevailing environmental conditions (e.g. long-term heavy grazing) and may be important for energy flow, nutrient cycling, wildlife habitat and soil stabilization. Their removal should not be contemplated without due consideration of what will replace them. Where soils, seed bank and vegetative regeneration potentials favour post-intervention re-establishment of unpalatable woody vegetation (Fig. 4.2), a long-term, carefully planned, strategically timed sequence of vegetation manipulation technologies may be required to drive the system back to some previous state (Scifres *et al.*, 1985; Noble *et al.*, 1991). However, chemical and mechanical manipulation may not be ecologically sound, socially acceptable, biologically effective or economically feasible on a large scale. Given the effort and expense required to reduce cover or biomass of unpalatable woody plants, it would be desirable to manage grazing lands to minimize their establishment. Experience to date suggests that the adage 'an ounce of prevention is worth a pound of cure' is certainly applicable. However, climatic variability and the unpredictable occurrence of extreme climatic events may effect rapid shifts in plant recruitment and mortality. These may unexpectedly promote grass die-off or enhance woody plant seed production and seedling establishment, leaving managers little opportunity to adjust animal numbers/composition or implement a prescribed burn. Socio-economic externalities may further interact to impede or constrain deployment of desired management practices.

KNOWING THE PAST, UNDERSTANDING THE PRESENT, PLANNING THE FUTURE

Causes for change cannot be addressed until we have an adequate understanding of the extent, pattern and rate of change that has occurred. Presumed composition and geographic distribution of presettlement vegetation is often used, either explicitly or implicitly, as a control or baseline to assess impacts of land use. Unfortunately, our knowledge of presettlement vegetation is sketchy; hence our foundation for determining the extent of the impact which livestock grazing may have had on soils and vegetation is often weak. Lack of historical perspective can place short-term studies in the 'invisible present', where a lack of temporal perspective can produce misleading conclusions (Magnuson, 1990). Assessments of stability and equilibrium are typically artefacts of the spatial and temporal scale at which we observe (DeAngelis and Waterhouse, 1987). Equilibrium states can occur at certain scales and contain disequilibrium at smaller scales. A historical perspective on vegetation dynamics is required to distinguish between short-term (seasonal, annual) fluctuation and long-term (decadal) directional change.

Original site factors/conditions significantly affect the structure and function of present-day vegetation and control the ways humans use sites and how natural processes affect them (Foster, 1992). For example, prehistoric faunal extinctions (Janzen, 1986; Owen-Smith, 1987), activities of early humans (Blackmore *et al.*, 1990) and historical fluctuations in native browsers and grazers (Sinclair, 1979) have significantly influenced the pattern and abundance of woody plants on modern landscapes. In southwestern North America, desert grasslands, which established under 300 years of cooler, moister Little Ice Age conditions, may be ill-suited for the warmer, drier climates of the last century and destined for replacement by xerophytic shrubs (Neilson, 1986). However, given the substantial 'biological inertia' of perennial plants, changes in vegetation may have lagged behind changes in climate and were not yet been manifested in the early 1800s. Grazing by livestock may have accelerated a vegetation change in progress at the time of settlement.

An accurate understanding of the extent and cause of changes which have occurred in systems grazed by livestock are necessary if we are to: (i) mitigate future undesirable impacts of grazing; and (ii) realistically assess restoration potentials. Conclusive studies linking human activity and ecosystem change require a combination of field experimentation coupled with comprehensive analyses of land-use history and long-term vegetation records. The subsequent sections review and evaluate techniques with the potential to reconstruct spatial and temporal patterns of vegetation and to relate these to environmental factors, land use and cultural conditions. Techniques in stable isotope chemistry, biogenic opals, dendroecology and historical aerial photography offer opportunities to generate spatially explicit reconstructions of vegetation history and to determine rates and dynamics of changes. As the number of such studies increases, our understanding of vegetation dynamics at landscape and regional scales will grow.

Traditional assessments of historical change in vegetation

Comparisons with relict stands

Relict stands on isolated mesas, on road or railway rights of way, in cemeteries or in long-term enclosures are often used as indicators of 'pristine' conditions. However, these: (i) are not necessarily representative of past communities or optimal conditions; (ii) may have been established after anthropogenic disturbances had influenced vegetation or soils; (iii) are typically small in size; or (iv) are confined to select topoedaphic conditions. This potentially produces artificialities in plant or animal production and population dynamics, disturbance regimes and microclimate, which can influence species composition or abundance. Extrapolation to other landscape units or sites within the region is therefore risky.

Historical records

Descriptions of vegetation from diaries of early explorers and settlers can be used to assess the historical impacts of livestock grazing (Malin, 1953). These are subject to many sources of error and bias (Forman and Russell, 1983). Discrepancies between present-day composition of relict stands and descriptions by early travellers cast doubt on the reliability of one or both as indicators of the extent or pattern of vegetation change. In addition, rates of change required to produce shifts in vegetation from the time of historical observation to the present may not agree with measured or ecologically realistic rates of change (Hoffman and Cowling, 1990; Palmer *et al.*, 1990).

Historical ground photographs

Matched or repeat ground photographs from early to recent times provide another means of visually comparing past and present vegetation. However, oblique, ground-level shots with narrow fields of view cover only small, select portions of a landscape, making it difficult to generalize about the areal extent or pattern of change (Bahre, 1991, p. 14). Shifting mosaics, resulting from cyclical replacements of species, may give the appearance of directional change, depending on the time-scale of observation (Remmert, 1991). Some portions of landscapes may be dynamic and responsive to changes in disturbance or environment, whereas other portions remain static, perhaps controlled by topoedaphic constraints. Serial photographs might therefore tell different stories, depending on when and where they were taken.

Stable carbon isotopes

Naturally occurring stable isotopes of carbon (^{13}C and ^{12}C) in CO_2 are differentially incorporated into vegetation in the process of photosynthesis. Plants with the C_3 photosynthetic pathway discriminate against ^{13}C to a greater extent than plants with the C_4 pathway (Bender, 1968). Tissues of plants with the C_3 pathway have a characteristic $^{13}C/^{12}C$ ratio (expressed as $\delta^{13}C$) of *c.* $-27‰$, whereas organic matter of C_4 plants is c. $-12‰$ (Smith and Epstein, 1971). Tropical and subtropical systems are dominated by C_4 grasses, their proportionate contribution to the flora decreasing with increasing latitude (Teeri and Stowe, 1976) and elevation (Tieszen *et al.*, 1979; Boutton *et al.*, 1980). Woody plants and herbaceous dicotyledons, with few exceptions, have the C_3 pathway. The $\delta^{13}C$ values of plant tissues are only modified slightly during decomposition. Accordingly, the proportionate contribution of C_3 and C_4 plants as carbon sources contributing to the tissues of heterotrophs and the organic matter of soils can be quantified by measuring the $^{13}C/^{12}C$ ratio in samples (see Tieszen and Boutton, 1989).

The isotopic 'memory' of soils can be queried by analysing the $\delta^{13}C$ of bulk soil organic carbon (SOC) or the carbon associated with various soil particle size-class fractions (sand, silt, clay), which differ in their turnover rates. The resultant signature is a direct reflection of the proportionate input of C_3 and C_4 vegetation to SOC integrated over long periods. If current vegetation has been a long-term occupant of the site, the SOC of soils should be comparable to that being put in by foliage, stems and roots. If a shift in the proportion of C_3 and C_4 plants has occurred, changes in SOC will lag behind changes in vegetation composition and reflect the input from previous plants long after they are gone. The extent to which $\delta^{13}C$ of vegetation and SOC are in equilibrium with each other is thus a quantitative indicator of vegetation history (Tieszen and Archer, 1990).

Changes in $\delta^{13}C$ with soil depth are an indirect measure of time, which can be corroborated by ^{14}C analyses. Quantification of $\delta^{13}C$ with depth can therefore provide a continuous record of vegetation composition from the past through the present. Palynological, archaeological or pack-rat midden techniques of vegetation reconstruction are site-specific and contain artificialities resulting from long-distance dispersal, differential preservation of materials and human or animal selection biases, which limit quantitative interpretation. In contrast, the $\delta^{13}C$ technique can be applied in a spatially explicit fashion and will quantitatively represent the proportionate biomass contribution of C_3 and C_4 plants to a given location over time. The following sections highlight some applications in grazed ecosystems.

Have historical increases in atmospheric CO_2 favoured C_3 shrubs over C_4 grasses?

It is difficult to assess the relative contribution of the various factors that may lead to directional shifts in vegetation. One novel explanation offered to account for historical vegetation change on rangelands centres around the hypothesis that increases in atmospheric CO_2 since the industrial revolution (*c.* 30%) have favoured C_3 plants over C_4 plants (Idso, 1992; Polley *et al.*, 1992; Johnson *et al.*, 1993). The historical displacement of C_4 grasses in tropical and subtropical regions by C_3 woody plants may not reflect changes in climate, fire or grazing regimes, but a differential response of their photosynthetic physiologies to increases in CO_2. This hypothesis is difficult to test, because assessments of vegetation change attributable to environmental effects on photosynthetic pathways are often confounded by life-form (e.g. grass vs. shrub vs. tree) or growth-form (e.g. evergreen vs. deciduous) differences in growth rate, phenology, canopy and root architecture and stress tolerance unrelated to C_3 or C_4 physiology. A more rigorous evaluation of the historical CO_2 enrichment hypothesis could be achieved if life-form or growth-form differences could be minimized to isolate the effect of photosynthetic pathway on historical changes in plant distribution and abundance.

Have there been historical shifts in C_3–C_4 distribution and abundance in accordance with the CO_2 enrichment hypothesis where plant life-form or growth-form differences are minimal? In the southwestern USA, the suffrutescent shrubs *Atriplex confertifolia* (shadscale) and *Ceratoides lanata* (winterfat) are widespread and achieve local dominance. *A. confertifolia* is C_4, whereas *C. lanata* is C_3. In other respects, these plants are quite similar. Both are members of the *Chenopodiaceae* and comprehensive studies have revealed few differences in productivity, water use efficiency and soil moisture utilization (Caldwell *et al.*, 1977). Dzurec *et al.* (1985) quantified $\delta^{13}C$ of soil organic matter along transects spanning contiguous, monospecific stands of each species. ^{13}C values of roots and soil organic matter under *Ceratoides* were in equilibrium with the current plant community. In contrast, $\delta^{13}C$ values of roots and soils under *Atriplex* portions of the transects were more negative than would be expected for a C_4-dominated community. Results indicate that the C_4 shrub, *A. confertifolia*, has increased in importance. This is contrary to predictions of the historical CO_2 enrichment hypothesis and suggests that other factors (Boutton *et al.*, 1994; Archer *et al.*, 1995) may have been more important in producing vegetation change on grazed rangeland.

Has livestock grazing contributed to regional desertification?

The origin and geographic extent of some biomes and their regional associations is the subject of frequent debate. In some cases, climatic and edaphic factors may determine the composition and extent of grasslands and savannas (Walker, 1987). In other instances, grasslands and savannas may be the result of forest and woodland conversion by indigenous people and settlers (Gadgil and Meher-Homji, 1985; Stott, 1991). The extensive grasslands of southern Africa may have existed for millennia, the result of climatic, edaphic or pyric determinants. Alternatively, these grasslands may be the result of extensive removal of trees by indigenous peoples and European settlers (Ellery and Mentis, 1992). Grazing in the drier regions of the country may have contributed to the expansion of arid Karoo shrublands into grasslands since settlement (Acocks, 1953). Thus, the extent of geographical change in shrubland and grassland boundaries, if any, is not clear (Hoffman and Cowling, 1990).

Bond *et al.* (1994) examined the geographical extent of South African grasslands using $\delta^{13}C$ techniques. The sites inspected were typically dominated (> 50% cover) by shrubs. Stable shrublands with little C_4 grass biomass were characteristic of the southwestern regions ($\delta^{13}C$ values strongly C_3 throughout the profile). Isotopic signatures indicated that the proportion of shrub biomass has increased in the central Karoo. Soils in the northeast were characterized by C_4 carbon at depths below 10 cm, indicating long-term past domination by C_4 grasses. Summer rainfall for the 11 sites across the region was strongly correlated with $\delta^{13}C$ values at each soil depth. Shrubs dominated where summer rainfall was below 150 mm; areas receiving above 280 mm were dominated by C_4 grasses.

The slope of the relationship between summer rainfall and $\delta^{13}C$ decreased with increasing soil depth, suggesting that the importance of summer rainfall in determining shrub–grass biomass has decreased over time. The results indicate that changes in land use (livestock grazing) have reduced grass abundance relative to the climatic potential.

This study supports the view that grass cover has declined under grazing pressure, but not that grasslands covered most of the central Karoo before settlement. This knowledge will facilitate evaluation of land management impacts on vegetation and temper expectations for range improvement and rehabilitation efforts. Establishment of grassland in portions of the Karoo which have historically been shrublands is probably unrealistic; efforts should be concentrated in the higher summer rainfall zones where grasses have historically flourished.

Resolution of conflicting assessments of historical woodland boundaries

Boundaries between grasslands and shrubland, woodland or forest systems can be dynamic or static, depending on soils and geomorphology, disturbance regimes, climatic stability and the spatial or temporal scales of observation (Longman and Jeník, 1992). In southwestern North America, post-Pleistocene, mid-latitude woody plant communities appear to have retreated upslope and to have been replaced by grasslands, a response to warmer, drier climatic conditions (Betancourt *et al.*, 1990). Historical–modern ground photographs suggest that *Quercus* woodlands in Arizona, USA have continued to recede upslope over the past century (Hastings and Turner, 1965). A shift toward a more xeric climate during this period is presumed to have caused this change. However, climatic records do not indicate significant changes in rainfall and other repeat photography suggests that *Quercus* woodland boundaries have been stable (Bahre, 1991). No clear generalizations emerge which enable us to infer how vegetation might have changed on landscapes for which there are no historical photographs.

$\delta^{13}C$ analysis of SOC provides the capability of assessing site-specific patterns of changes in grass–woody plant abundance. When applied to soils from stands in southeastern Arizona, it was determined that C_3 *Quercus* and *Prosopis* trees occupied soils whose isotopic signature reflected prior domination by C_4 grasses (McPherson *et al.*, 1993). Discrepancies in isotopic composition between the current vegetation and SOC indicate that patches dominated by woody plants are recent. The isotopic data provide direct evidence that woodland margins have been advancing at this site. This is contrary to historical photography, which suggests that woodland boundaries have been either static or retreating.

Historical accounts and archaeological records often indicate that woody vegetation was present in grasslands, but restricted to riparian corridors and intermittent drainages and, as gallery forest stands, associated with escarpments and steep topography. The former sites could have favoured woody vegetation by affording deeper soils and better water relations, the latter by conferring a degree of protection from fire. It is inferred that woody plants have subsequently spread from these historical enclaves and increased in abundance in other portions of the landscape. $\delta^{13}C$ analysis of SOC supports this contention in some areas, but not in others. For example, along the Niobrara River and its short tributary streams, past woodlands appear to have been more narrowly restricted to lower canyon slopes than the current woodlands (Steuter *et al.*, 1990). Isolated islands of woodland vegetation were also identified within grasslands on the upper canyon slopes prior to European settlement. These historical patches have since been engulfed by woodlands expanding from the lower slopes. In this situation, $\delta^{13}C$ analyses confirm historical observations. In other instances, assumptions of historical occupancy of certain landscape elements by woodlands do not appear valid. $\delta^{13}C$ reconstructions in southern Texas savannas indicate that closed-canopy woodlands of present-day intermittent drainages were dominated by C_4 grasses (Boutton *et al.*, 1993). This represents a case where vegetation history would have been incorrectly inferred from generalizations based on historical reports.

Grassland-to-woodland succession: corroboration of mechanisms

An understanding of successional processes and identification of states and transitions is of interest in cases where vegetation changes are thought to have occurred. A chronosequence of bush clump development in the succession from grasslands to woodland has been proposed for savanna parklands of southern Texas, USA (Archer *et al.*, 1988). Their scenario is based upon inferences derived from 'space-for-time substitution' studies of vegetation structure (Van der Maarel and Werger, 1978). It is desirable to independently corroborate the proposed chronosequence, because inferences from this static approach can be misleading (Austin, 1980; Shugart *et al.*, 1981). If shrub clusters have been a long-term constituent of the landscape, the $\delta^{13}C$ of SOC beneath them should fall in the –27 to –32‰ range. However, if C_3 shrubs have displaced C_4 grasses: (i) SOC $\delta^{13}C$ values would be less negative than –27 to –32‰; (ii) the degree of departure from the expected $\delta^{13}C$ would decrease as time of site occupancy by shrubs increases; and (iii) SOC $\delta^{13}C$ values would become less negative with depth along the chronosequence.

An analysis of SOC $\delta^{13}C$ confirmed these predictions (Archer, 1990). The SOC beneath herbaceous zones was strongly C_4 and reflected the composition of the current vegetation throughout the profile ($\delta^{13}C = -14$ to -18‰). In contrast, mean $\delta^{13}C$ values in the upper horizon of soils beneath clusters at early and late stages of development was –21 and –23‰, respectively, reflecting the passage of time and development of *Prosopis* plants and clusters. Among soils supporting woody vegetation, the contribution of C_3-derived carbon decreased with depth to 60 cm, converging on the values observed for the herbaceous zones. The observed SOC $\delta^{13}C$ values provide direct evidence that woody plants have displaced grasses on these landscapes and that the chronosequence proposed by Archer *et al.* (1988) is reasonable. Further, they lend credibility to models (Archer, 1989;

Scanlan and Archer, 1991) which indicate that succession from grassland to woodland began about 100–150 years ago.

Biogenic opals

Opaline phytoliths (SiO_2) are formed in plants when silicon passively enters the transpiration stream and precipitates in foliage. These microscopic particles, also known as biogenic opals, plant opals, silica bodies or bioliths, are added to the soil via litter fall. Grasslands commonly contribute five to 20 times more opal than woody plant communities, and the shapes and sizes of opals derived from grasses differ from those derived from woody plants. Accordingly, soil opals have been used to detect changes between grass and woody plant domination (Kalisz and Boettcher, 1990) and to document the stability of boundaries between adjacent grassland and woodland communities (Kalisz and Stone, 1984; Fisher *et al.*, 1986). The morphology of opals produced by grasses in the Chloridoid, Panicoid and Festucoid tribes differ, and their relative abundance in the soil can be quantified and compared with the extant vegetation. Opal phytoliths are highly resistant to weathering, and problems of long-distance transport, which occur with pollen-based reconstructions, are minimized. Some care is required in interpreting phytolith assemblages, as their composition can be affected by decay, fire, herbivory and fluvial/colluvial deposition (Piperno, 1988; Fredlund and Tieszen, 1994). As with the $\delta^{13}C$ approach, analysis of soil opals can be conducted in a spatially explicit fashion, both by soil depth and across landscapes or regions. In contrast to $\delta^{13}C$ analysis of SOC which provides only a low resolution of compositional change (C_3 vs. C_4 plants), biogenic opals can be used to determine shifts between tallgrass and shortgrass composition (Twiss *et al.*, 1969), replacement of perennial grasslands by annual grasslands (Bartolome *et al.*, 1986) and grassland vs. woodland composition shifts in temperate zones where there are few C_4 plants.

Dendroecology

Spatially explicit changes in grass–woody plant abundance can be documented by $\delta^{13}C$ or opal phytolith analysis, but they do not provide detailed time lines for the rates and dynamics of change. ^{14}C dating can be employed, but this is of limited use because of the expense, low precision and poor resolution, particularly for recent (the past 200 years) carbon. Analysis of annual rings of woody plants is a powerful tool in reconstructing the rates and dynamics of plant growth and stand history. Traditionally, tree ring research has focused on long-lived forest species with an emphasis on climate reconstructions. Ecological applications quantifying fire history and differences in species growth and population structure in relation to soils, disturbance, succession and annual rainfall are accumulating (Henry and Swan, 1974; Stewart, 1986; Swetnam and Lynch, 1989; Johnson and Young, 1992; Villalba *et al.*, 1994). Although the potential exists to use techniques in dendroecology in shrub- and woodland systems (Ferguson, 1964; Roughton, 1972; Wyant and Reid, 1992; Keeley, 1993), surprisingly few studies have been undertaken.

No rings, false rings, double rings

Utilization of woody plants for 'dendroecology' requires species that produce distinguishable rings, which can be dated with dendrochronology, and attain sufficient age to provide the time control required for a particular investigation (Fritts and Swetnam, 1989). Species vary widely in the extent to which growth rings are discernible, and growth anomalies such as 'missing rings' and 'false rings' occur. It is necessary to verify the annual nature of ring deposition if techniques in dendrochronology are to be reliably applied. This is particularly important for woody plants, whose ranges extend into tropical and subtropical environments, where temperatures are mild year-round and patterns of ring deposition may be in response to wet and dry periods (Jacoby, 1989). Many dryland woody plants are also capable of vegetative regeneration from lignotubers, below-ground stems or roots following disturbance. As a result, ages of current stems or trunks (ramets) may not necessarily reflect the antiquity of the plant (genet), which may produce many generations of stems (Table 4.2) (Wellington *et al.*, 1979; Vasek, 1980; Grimm, 1983). Present-day stems of such plants may contain information on site history acquired during their lifetime, but do not necessarily represent the potentially longer history of plant occupancy.

In many dryland systems, the suitability of woody plants for tree ring analysis is not known and must be ascertained. Flinn *et al.* (1994) determined that the dryland tree legume *P. glandulosa* produced annual rings across a broad north–south temperature gradient and east–west annual rainfall gradient by examining rings on

Table 4.2. Comparison of *Prosopis glandulosa* (mesquite) stem (ramet) ages determined from annual ring counts with estimated plant (genet) age determined from ^{14}C ageing of underground burls or lignotubers which gave rise to those stems (S. Archer, unpublished data). Lignotubers of plants 1–4 dated 'modern' (< 200 years) in accordance with trunk ages. However, the burl of plant 5 was of significantly greater antiquity than the trunk it produced. Ages determined from annual ring counts of above-ground stems may not reflect the true age of woody plants, which vegetatively regenerate after disturbance.

	Estimated age years	
Plant	Lignotuber	Trunk
1	190 ± 75	73 ± 1
2	210 ± 80	81 ± 1
3	50 ± 53	73 ± 6
4	185 ± 75	79 ± 6
5	510 ± 75	67 ± 3

plants from stands with known management histories. They also found that special sanding and staining techniques helped highlight annual rings of *P. glandulosa*.

Stands of known age may be impossible to locate. How, then, can annual ring production be validated? McAuliffe (1988) utilized a novel approach whereby he scarred basal stems of *Larrea tridentata* by removing a 1-mm strip of outer bark and cambium. Secondary xylem deposition subsequently occurred around the entire perimeter of the trunk, except where the cambium was removed. The scar thus provided a permanent marker distinguishing the wood deposited before and after the cambium was removed. Cross-sections were subsequently harvested at various dates after scarring, the amount of xylem deposition since the date of cambium scarring was determined, and annual ring deposition was verified.

Ecological applications in rangelands

Dendroecology can be used, where annual ring production has been confirmed, to quantify regional synchronization between climatic conditions and wildfire (Swetnam and Lynch, 1989), to reconstruct local fire histories (Arno and Wilson, 1986) and to demonstrate how declines in fire frequency associated with the advent of livestock grazing have been accompanied by an increase in woody plant establishment in grasslands and savannas (Madany and West, 1983; Arno and Gruell, 1986; Savage and Swetnam, 1990). Timing of woody plant establishment and rates and patterns of stand development in grazed systems have also been quantified using dendrochronology. McPherson and Wright (1990) used dendrochronology and climatic records to demonstrate that consecutive years of above-average rainfall were required to trigger *Juniperus pinchotii* establishment on western Texas grasslands; one wet year is required for seed production and a second wet year for seedling establishment. Steinauer and Bragg (1987) documented accelerated rates of tree establishment in prairies since settlement and showed the rates of establishment were greatest on north-facing slopes. Sequential invasion of *Artemisia nova* shrublands, first by *Juniperus osteosperma* and later by *Pinus monophylla*, was quantified by Blackburn and Tueller (1970), using tree ring analysis. Such studies indicate the utility of dendroecology for assessing site-specific changes in grass and woody plant abundance. Given their potential for providing unique ecological information, annual ring production in arid and semiarid shrub and arborescent species should be thoroughly investigated.

Repeat aerial photography

The areal extent of spatial reconstructions of vegetation change based on $\delta^{13}C$, opal phytoliths and dendroecology are limited by the time, labour and financial costs associated with collecting and processing of samples. When available, historical aerial photographs are a means of obtaining more extensive, landscape-level assessments of rates, dynamics and patterns of change in herbaceous and

woody plant distribution. Constraints on the use of sequential aerial photography include: (i) historical resolution (photographs seldom predate the 1930s or 1940s); (ii) frequency (time elapsed between successive photo dates is variable and not necessarily related to ecologically significant events); (iii) spatial resolution (photography may not be sufficiently detailed to detect change, or the scale may vary between dates, making it difficult to obtain accurate comparisons); (iv) image quality (quality of imagery may be insufficient to enable accurate determinations and the quality may vary between dates); and (v) parallax distortion, tilt and terrain effects (Bolstad, 1992). However, when available, sequential aerial photography can be used to quantify and integrate the outcome of interactions among short-term, small-scale processes and climatic fluctuation on large-scale, long-term vegetation patterns. As such, it provides a useful tool for quantifying vegetation dynamics on landscapes at spatial and temporal scales relevant to perennial plant life histories, secondary succession and land management.

States, transitions and boundary dynamics

As discussed previously, management and conservation of grazed rangelands depends on knowledge of likely vegetation states and transitions affecting those states (Fig. 4.2). Application of state and transition models in research and management are constrained by a lack of quantitative details regarding the identification of states and probabilities of change between states on a particular landscape unit. One approach involves the computation of transition probabilities. Matrix projection models have been traditionally utilized to analyse, interpret and project plant demography and life-cycle attributes (Caswell, 1989). Applications on rangelands include analysis of grass demography with respect to fire (Silva *et al.*, 1991), grazing and drought (O'Connor, 1993) and fertilization and seeding (Scott *et al.*, 1990). The approach has also seen limited use in predicting species interactions and succession with repeated, ground-based measurements (Redetzke and Van Dyne, 1976; Austin, 1980; Burrows *et al.*, 1985) or size/age/fecundity relationships (McAuliffe, 1988; Yeaton and Bond, 1991). As the following case-studies indicate, this approach can be used in conjunction with aerial photography in lieu of long-term permanent plot data to identify, quantify and predict patch and community 'states and transitions' at spatial and temporal scales pertinent to succession and landscape management (see Hall *et al.*, 1991, for applications in satellite imagery).

Changes in savanna tree cover

To quantify thornbush encroachment in a heavily grazed Botswana shrub savanna, Van Vegten (1983) distinguished and mapped eight woody plant canopy cover classes (ranging from < 1% to > 75%) on aerial photographs from 1950, 1963 and 1975. The woody plant biomass represented by each cover class was estimated from field sampling. Average woody plant biomass nearly tripled on this site over the 25-year period. A similar increase in woody plant cover was noted in heavily grazed subtropical savannas in southern Texas, USA (Fig. 4.3a). Drought and grazing interacted to influence the dynamics of woody plant encroachment (Archer, 1994), which was spatially variable across the landscape (Archer, 1995a). The outcome of these interactions was quantified by aerial photography at spatial and temporal scales not possible using ground-level clipping experiments and monitoring regimes.

Reconstructing the past, predicting the future

The successional development of woodland communities depicted in Fig. 4.3a has been elucidated (Archer *et al.*, 1988) and $\delta^{13}C$ analyses confirm that woody plant complexes occupy sites once dominated by C_4 grasses (see under Stable Carbon Isotopes above). Is it possible that successional processes producing a shift from grassland to woodland could have occurred since settlement of this area in the mid to late 1800s? To address this question, rates of canopy expansion of woody clusters representing successional age states were determined from historical aerial photography, related to annual rainfall and modelled to determine woody plant size–age relationships over an array of annual precipitation regimes (Archer, 1989). The model predicted that sizes of present-day woody plant assemblages could have been achieved within the past 100 years under the annual rainfall regimes characteristic of the region. Estimates of woody plant growth rates derived from canopy expansion measurements on aerial photos (0.8–1.9 mm year^{-1} radial trunk growth) were consistent with measurements from dendrometer bands over 6 years (0.2 to 2.0 mm year^{-1}) (S. Archer, unpublished).

Use of aerial photography to parameterize woody plant growth models and determine age-class distributions provides a population biology perspective on woody plant encroachment and stand development, but does not represent the net result of spatial variation in recruitment, growth and mortality of plants across the landscape over time. For this perspective, Scanlan and Archer (1991) used aerial photography to quantify probabilities of transition between seven vegetation age states corresponding to previously defined seral stages in succession from grassland to woodland. These transitions were used in a matrix projection model to assess how landscape composition might vary over time. Vegetation states were assessed in grids of 20 m × 20 m cells superimposed on aerial photos. Transitions were calculated for a drought period (1941–1960) and a normal annual rainfall period (1960–1983) and were found to differ significantly between these two periods. Subsequent theoretical analyses indicated the analytic solutions of this non-homogeneous matrix projection approach provided a reasonable explanation of observed vegetation dynamics (Li, 1995). Past and future landscape structure was modelled by randomly selecting 'normal' and 'dry' transitions at 20-year time steps. The model was run for a series of rainfall scenarios, ranging from 'normal' chosen at each time step to 'dry' chosen at each time step. Forward and reverse simulations were used to project and reconstruct vegetation change. Linkage of

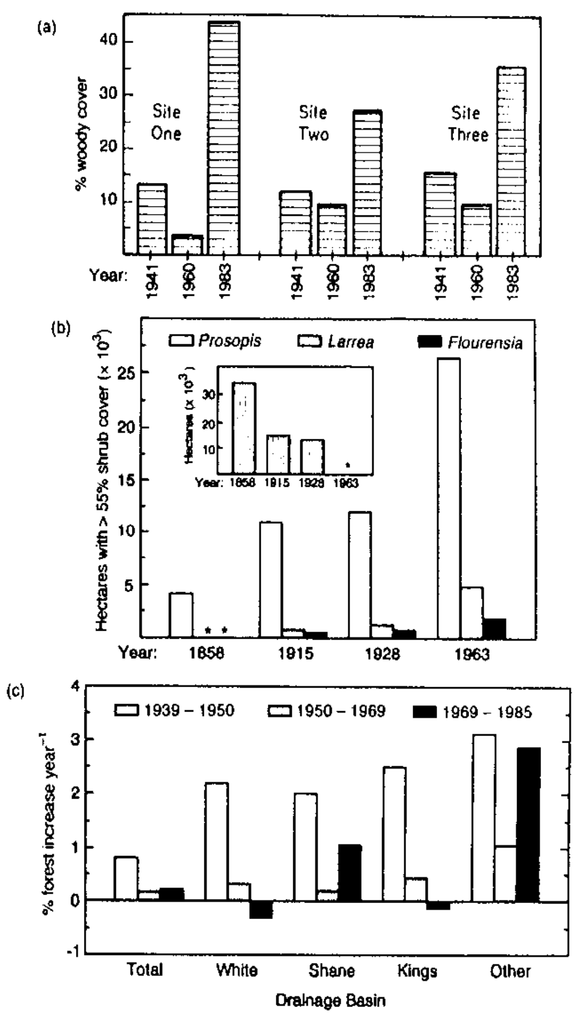

Fig. 4.3. Changes in woody plant abundance in grasslands and savannas representing three climatic zones in North America have been non-linear and spatially variable. (a) *Prosopis–Acacia* savanna in southern Texas; a severe drought occurred in this region in the 1950s (from Archer *et al.*, 1988); (b) Chihuahuan Desert, New Mexico. Insert depicts acreage with no woody plants. Asterisks denote zero acres (from Buffington and Herbel, 1965); and (c) gallery forest expansion rates in a Kansas tallgrass prairie. Primary woody plants were *Quercus*, *Celtis* and *Ulmus* (from Knight *et al.*, 1994).

this successional model to an ecosystem biogeochemistry model has enabled evaluation of the landscape-level impacts of grazing on carbon and nitrogen dynamics (Hibbard, 1995).

Shifting mosaics and boundary dynamics

Historical aerial photographs substantiate the contention that riparian corridors, intermittent drainages and escarpments are an important source of propagules for the lateral spread of woody plants into uplands with the advent of livestock grazing and fire suppression. Knight *et al.* (1994) document an increase in the number and acreage of gallery forest patches in tallgrass prairie in North America between 1939 and 1985 (Fig. 4.3(c)). Rates of increase were not linear, nor were they uniform from one drainage basin to another.

Biological interactions acting in concert with disturbance and variation in topography and substrate may produce complex transitional changes among community mosaics. These changes can be difficult to evaluate because they occur at spatial scales and over time-frames not amenable to traditional experimentation or monitoring. Patterns of cyclic succession that occur over decadal time-frames and at landscape spatial scales may be erroneously interpreted as directional succession if observations are made over shorter time intervals at the patch level. However, by comparing changes in mosaic patterns on landscapes with different management histories, some insights regarding land-use influences on rates of transition among vegetation states can emerge.

A recent example involves quantification of shifts among grassland, coastal sage scrub, chaparral and oak woodland communities in central coastal California (Callaway and Davis, 1993). Shifts were determined by comparing aerial photographs from 1947 and 1989. Geomorphic substrate, soil type, aspect and topography were recorded in randomly located 'plots' on the 1947 photographs. Vegetation cover was classified in the plots distributed across areas which differed in their fire and grazing history and compared with that recorded for the same plots relocated on 1989 photographs. A matrix projection model based on transition probabilities was then developed. Results (Fig. 4.4) indicated that: (i) transitions among community types were high, even in the absence of grazing and burning; (ii) fire reduced the invasion of grassland by coastal sage scrub, converted coastal sage scrub to grassland and limited oak woodland expansion; (iii) effects of fire on grass–woody plant ratios varied with soil type; (iv) grassland to coastal sage to oak woodland to grassland transitions occurred, suggesting cyclic succession; (v) chaparral shrubland and oak woodland rarely replaced grassland directly, but both rapidly replaced the coastal sage scrub, which directly replaced grassland; and (vi) livestock grazing had little influence on transitions from grassland to coastal sage scrub to oak woodland.

As the above studies indicate, aerial photography can help elucidate and quantify the outcome of interactions between biology, disturbance and the physical environment (see also Richardson and Brown, 1986; Williams *et al.*, 1987).

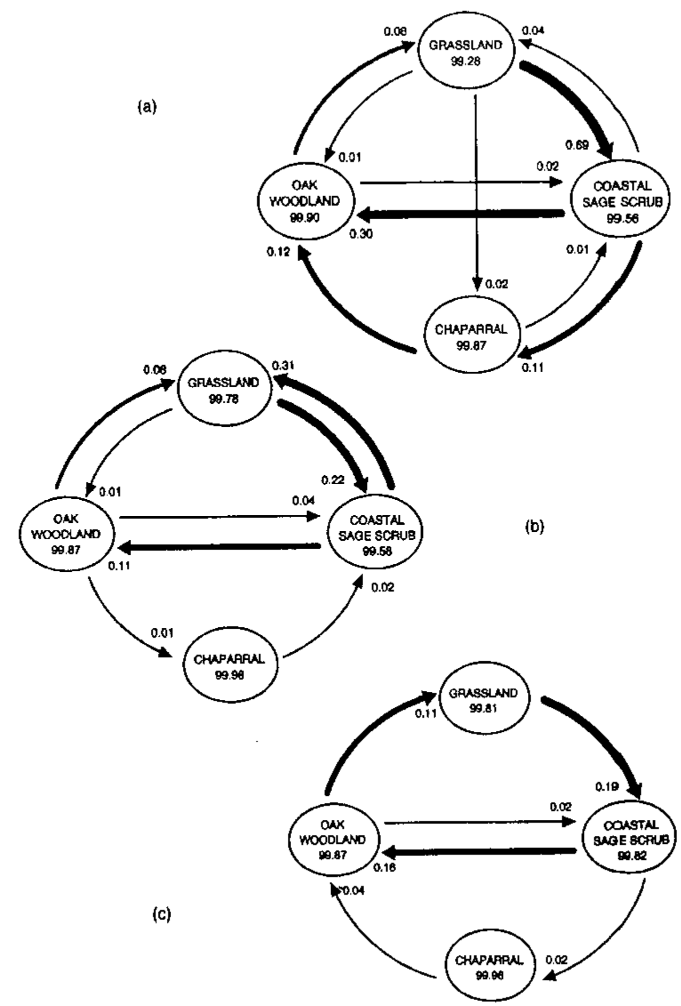

Fig. 4.4. Annual transition rates among vegetation states with different grazing and burning histories in central California determined from aerial photography (1947 vs. 1989). Numbers in ovals represent the probability, as a percentage, that a given community will remain the same; numbers on the arrows estimate the probability that a community will change in the indicated direction. (a) No fire, no livestock grazing; (b) fire, no livestock grazing; and (c) livestock grazing, no fire (from Callaway and Davis, 1993).

SUMMARY

An understanding of factors affecting the composition and productivity of communities through time is of fundamental interest to plant ecologists. However, the world's plant cover is complex and variable and much is not readily accessible for scientific study. We are typically forced to extrapolate our knowledge of plant and community response to grazing obtained from short-term, small-scale studies with little understanding of their historical context or with little knowledge of how to apply them across a landscape, to other landscapes or over longer time periods. Expansion and proliferation of unpalatable woody plants is often associated with livestock grazing in arid and semiarid regions. However, there has been little quantification of the rate, dynamics, pattern and extent of these vegetation changes. As a result, we are often left to speculate whether this sort of vegetation change has occurred and what the proximate causes might have been.

In many instances confusion, contradictions or inconsistencies regarding impacts of grazing on vegetation composition and dynamics can be resolved if: (i) site or land-use history is known; and (ii) processes are expressed in a spatially explicit manner which considers soils, topography and geomorphology at time intervals appropriate for evaluation of species interactions, plant life histories and climatic variation. Stable carbon isotope chemistry, biogenic opal inventories, dendroecology and repeat aerial photography are underutilized tools capable of providing information needed to reconstruct, understand and interpret vegetation dynamics in rangeland ecosystems. Used alone or in concert, these tools enable quantification of past changes in plant distribution in a spatially explicit framework over time-frames and spatial scales relevant to management of grazed landscapes. As databases generated from studies using these approaches accumulate, we can explicitly refine and better evaluate hypotheses and conceptual models of vegetation dynamics in grazed ecosystems. When used in conjunction with mechanistic investigations of factors influencing patterns and processes at plant and population levels of resolution, demographic data, biogeochemical simulation modelling and climatic records, a more complete, accurate and spatially explicit representation of grazing impacts on landscape structure can emerge. Armed with a more accurate historical perspective, we can design better monitoring schemes, more objectively evaluate land management impacts on vegetation, improve our predictive capabilities and temper our expectations with regard to range improvement practices and rehabilitation efforts.

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