SHRUBLAND ENCROACHMENT IN SOUTHERN NEW MEXICO, U.S.A.: AN ANALYSIS OF DESERTIFICATION PROCESSES IN THE AMERICAN SOUTHWEST

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> *More and more the conviction grows that we are not merely at one stage of a cycle repeating itself, but that the past eighty years have witnessed the evolution of a significant new vegetation put together out of the floristic remains of the old. There is no sign that the evolution has seen its full development yet, or is slackening its pace.* (Hastings and Turner, 1965)

Abstract. The area dominated by the shrubs creosotebush *(Larrea tridentata)* and mesquite *(Prosopis glandulosa)* in the American southwest has increased severalfold over the last century, with a corresponding decrease in areal coverage of productive grasslands and increased surface soil erosion throughout the region. The factors thought to be responsible for this regional shift in vegetation are: (1) overgrazing by domestic livestock; (2) fire suppression; and (3) historical changes in climate. We examine the evidence concerning each of these factors and develop a synthetic model outlining the principles affecting shrubland encroachment, which focuses on life history characteristics of the dominant shrubs and a number of positive biotic and edaphic feedback mechanisms contributing to their establishment and persistence. We conclude that the expansion of shrub dominance that has occurred over the last century may have been triggered by extreme livestock overgrazing at the end of the nineteenth century, which coincided with rainfall regimes that were unfavorable for perennial grass growth. Hence, the landscape we observe today may be a product of positive feedback mechanisms triggered over a century ago by management practices that were uninformed with regard to the importance of historical climate patterns and the life history characteristics of important rangeland species. Our consideration of these issues also addresses potential land surface – climate interactions that could occur as a result of regional alterations in vegetation dominance and physiognomy.

1. Introduction

During the last century a dramatic compositional and physiognomic change has occurred in the dominant vegetation of the American southwest (see above quote). Early visitors and explorers to the area now encompassed by southwest Texas, New Mexico, and southern Arizona described a verdant landscape supporting vigorous stands of perennial grasses and associated forbs, later classified as desert grassland

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(e.g., Branson, 1985; Gross and Dick-Peddie, 1979; Humphrey, 1958; Whitfield and Beutner, 1938). Today, much of this area is shrubland dominated by creosotebush *(Larrea tridentata)* and mesquite *(Prosopis glandulosa)*. Coincident with this shift in vegetation dominance has been a marked increase in soil erosion and stream channel cutting (i.e. arroyo cutting; see Bryan, 1928; 1925), and increased coppice dune formation in the sandier soils throughout the region.

Three hypotheses have been offered to account for these changes: (1) degradation of the range through domestic livestock grazing and increased rodent activity (Buffington and Herbel, 1965; Hennessy *et al.*, 1983; Norris, 1950); (2) fire suppression due largely to removal of potential fuels by grazing (Humphrey, 1958); and (3) changes in climate affecting temperature and precipitation patterns (Leopold, 1951a; Cooke and Reeves, 1976). While not well quantified, there is some evidence to indicate that reduction in vegetation cover and exposure of soil may have local and regional climatic effects through increased surface temperatures in severely affected areas (Balling, 1988).

Past works have seldom attempted to synthesize all of these factors into a coherent model of desertification processes for this region (but see Schlesinger *et al.*, 1990). Such a model is essential for understanding the interactive factors (e.g., floral and faunal life history characteristics, land use history, historical climatic patterns) responsible for shrub invasion and increased shrub cover. Our synthesis addresses these and other issues from the perspective of landscape ecology, an emerging paradigm concerned with the factors responsible for heterogeneity in ecosystem pattern and process. We identify unresolved questions that must be addressed in order to determine the potential effects of climate change in the American southwest.

2. Patterns of Vegetation Change

Creosotebush and mesquite have been present in the American southwest for at least 4000 years (e.g., McCraw, 1985; Van Devender and Spaulding, 1979), but were probably only locally dominant. Gross and Dick-Peddie (1979) and York and Dick-Peddie (1969), using historical journal records and General Land Office range survey notes, concluded that until early in the twentieth century most of southern New Mexico was dominated by perennial grass cover with mesquite present in some drainageways and near old Indian campsites, while creosotebush was restricted to gravelly, well-drained soils of the foothills (see also McCraw 1985).

The rate of shrubland encroachment over the last several decades has been examined locally for the Jornada Experimental Range in south-central New Mexico (Buffington and Herbel, 1965; Hennessy *et al.*, 1983), and regionally for the extreme southwestern counties of New Mexico (i.e. the Bootheel; McCraw, 1985). Each of these studies relies on early range survey records for its baseline, followed by more recent inventories that document increased shrub cover. While the Jornada study includes changes in all types of shrub *vs* grassland cover, the Bootheel study examines only creosotebush invasion.

Figure 1a illustrates the changes that have been quantified in various vegetation types for the Jornada Experimental Range (Buffington and Herbel, 1965). The total area included in this study is 58 468 ha, which since 1915 has gone from 43% shrub-occupied to 100% shrub-occupied. Their data also show that mesquite has increased in dominance at the expense of grassland and has displaced creosotebush mixtures in some areas. For example, in 1963 mesquite accounted for 63% of the total shrub coverage on the Jornada, but represented only 53% of the total in 1915.

Figure 2 illustrates the change that has occurred in creosotebush dominance in the Bootheel region of New Mexico (McCraw, 1985). From 1899 onward, creosotebush has come to dominate an additional 565 300 ha, or approximately 27% of the area shown.

For the entire American southwest, estimates of mesquite and creosotebush

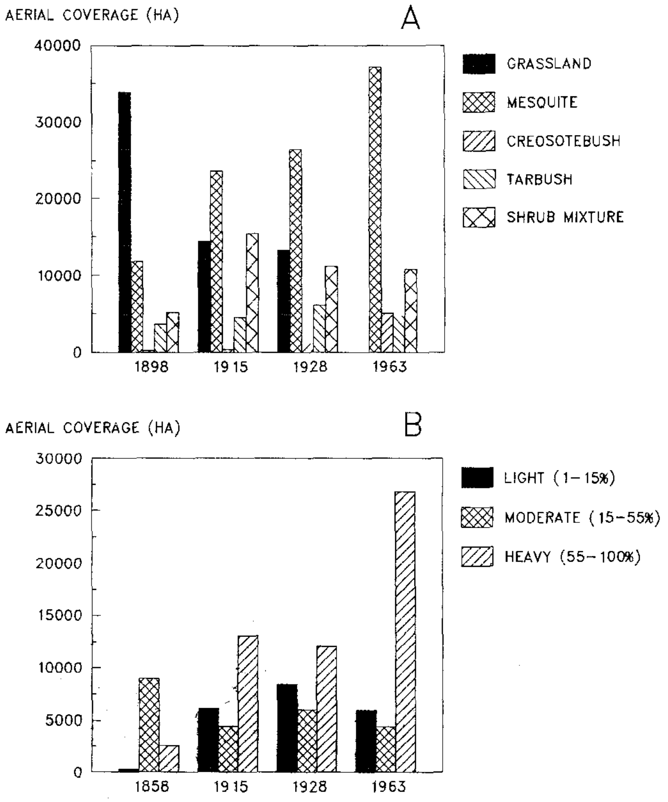

Fig. 1. Summary of change in the areal coverage (ha) of several vegetation types on the Jornada Experimental Range (based on data in Buffington and Herbel, 1965). (A) Total coverage of grassland and shrubland categories. (B) Change in areal coverage of several shrub density categories for mesquite.

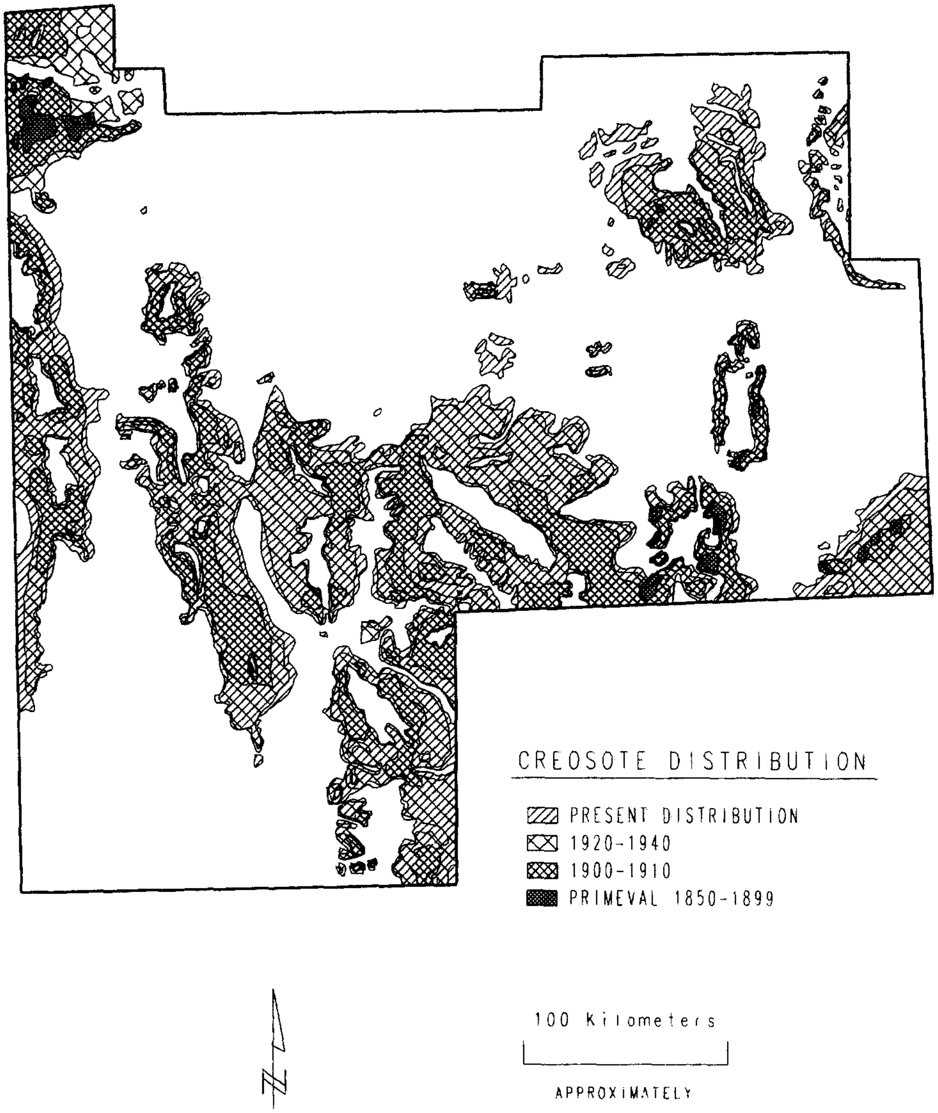

Fig. 2. Representation of change in creosotebush dominance for the extreme southwestern portion of New Mexico, U.S.A. (based on data in McCraw, 1985).

coverage indicate that by the late 1950's, mesquite had come to dominate 38 million ha across the region, with creosotebush dominant on about 19 million ha (Platt, 1959). A county-by-county statewide survey of New Mexico (Table I; Garrison and McDaniel, 1982) estimated areal coverage of mesquite to be about 7.58 million ha and that of creosotebush to be about 3.68 million ha. Of the total 11.26 million ha occupied by creosotebush and/or mesquite, about 47% is report-

TABLE I: Areal coverage (10^6 ha) of mesquite and creosotebush in New Mexico based upon county surveys (Garrison and McDaniel 1982)

Type	Coverage (10^6 ha)			
	Light[a]	Moderate[b]	Dense[c]	Total
Mesquite				
Warm Desertic soils	2.44	0.87	0.95	4.26
Central/Southern High Plains	1.28	1.19	0.85	3.32
Total Mesquite	3.72	2.06	1.80	7.58
Creosotebush[d]	1.61	0.88	1.19	3.68
Total	5.33	2.94	2.99	11.26

[a] Canopy cover of 5–15%.
[b] Canopy cover of 15–24%
[c] Canopy cover of 25% or more
[d] Includes areas of tarbush (*Flourensia cernua*), which commonly occurs with creosotebush.

ed to have a light canopy cover (5 to 15%), 26% moderate cover (15 to 24%), and the remaining 27% dense shrub cover (> 25%).

In addition to range extension, creosotebush and mesquite encroachment may continue through filling-in of areas now supporting light or moderate densities of these species (Gardner, 1951; Johnston, 1963; McCraw, 1985). For example, the inventories for the Jornada Experimental Range cited earlier document conversion of light cover classes of mesquite to dense classes (Figure 1b; Buffington and Herbel, 1965; Hennessy *et al.*, 1983). From 1915 to 1963, total mesquite cover doubled on the Jornada, while the proportion of dense mesquite (greater than 55% relative cover, where relative cover refers to percent of total perennial plant cover) increased from 55 to 72% of the total. There were concomitant shifts in light (15% or less relative cover) and moderate (15 to 55% relative cover) cover classes from 26 and 19% of the 1915 total to 16 and 12% of the total mesquite coverage in 1963.

The countywide surveys (Table I) reveal that of the total 11.26 million ha in creosotebush and mesquite, only about 26% are classified in the most dense cover class. This suggests that a maximum of 8.27 million ha in New Mexico (the areal coverage of light plus moderate cover categories) is vulnerable to further increases in shrub density. As shown in Table I, the potential for increased shrub dominance is greater for mesquite (5.78 million ha, or 76% of its range) than for creosotebush (2.49 million ha, or 68% of its range). However, these estimates are inflated by an unknown amount since in some areas mesquite and creosotebush presently co-occur and through time one or the other species may become dominant, or density increase may not occur for either species in some areas where they are codominant.

3. Contributing Factors

Grazing

Indian cultures that were largely hunter-gatherer and locally agrarian occupied the American southwest for thousands of years prior to Spanish colonization. While aboriginal populations had significant impacts on their local and regional environments, a significant qualitative and quantitative change in human impacts on regional ecosystems began in the 1500's when the Spanish introduced domestic livestock grazing, and this impact continues to the present (see Branson 1985).

Livestock grazing was introduced in northern Mexico and southern Arizona in concert with the establishment of Spanish missions (Hastings and Turner, 1965). It is likely that several hundred thousand head of livestock were brought into the southwest by the late 1700's. Early Anglo explorers and military expeditions reported that many of these Spanish and Mexican ranching operations were abandoned by the early 1800's, leaving thousands of cattle roaming wild across the area (Hastings and Turner, 1965).

What is most striking from the reports of parties visiting the American southwest during the mid-1800's is the amount and condition of grass cover they observed. Journals going back to the late 1840's and forward (reviewed by Humphreys, 1958; Buffington and Herbel, 1965; Gardner, 1951; Hastings and Turner, 1965; and Leopold, 1951b) each describe broad plains with vigorous grass growth across much of New Mexico and southern Arizona. Brush cover was observed to be locally dominant in valley bottoms and drainageways (mesquite), or on coarse soils of the uplands and foothills (creosotebush).

Livestock census records from the early 1880's reveal a rapid influx of cattle and sheep to the southwestern rangelands coincident with the arrival of the railroads and suppression of Indian raids (see Hastings and Turner, 1965). In New Mexico, early livestock records estimate less than 200 000 cattle and about 1.6 million sheep in 1870, peaking during the late 1880's at about 1.4 million cattle, and 4.6

TABLE II: Summary of areal coverage of soil associations in New Mexico relative to their ability to support creosotebush (based on data presented in Maker *et al.*, 1974; see also Figure 3)

Suitability	Area ($\times 10^6$ ha)
Mostly suitable	1.8
Marginal and mixed	
Suitable	1.3
Unsuitable	1.3
Mostly unsuitable	3.4
Total	7.8

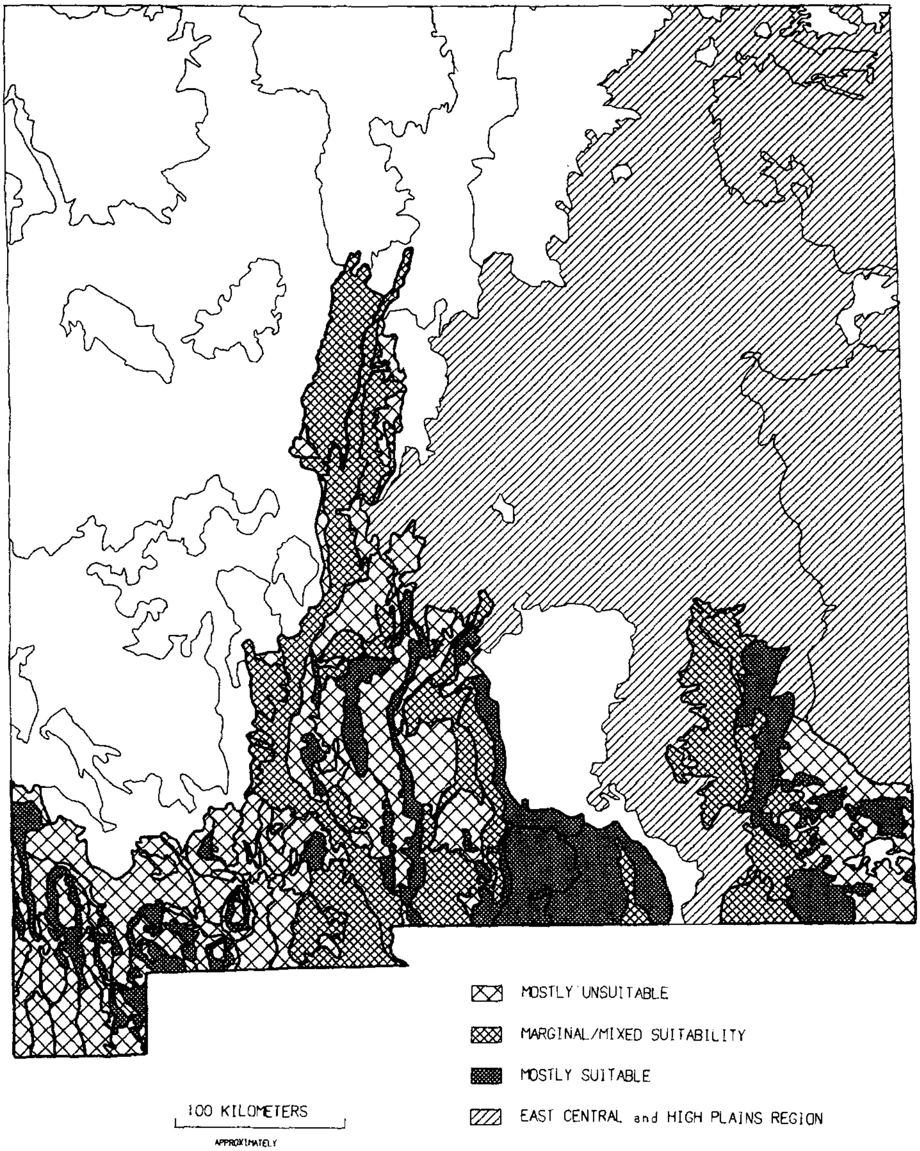

Fig. 3. Distribution of soils in New Mexico, U.S.A., that are vulnerable to mesquite or creosotebush invasion (based on Maker *et al.*, 1974). Suitability classes based upon soil properties affecting creosotebush establishment (see text for further explanation).

million sheep (Schickedanz, 1980). Drought and severe winters in the late 1880's and early 1890's combined to decimate the grazing industry throughout the southwest, with mortality estimates as high as 85 percent in some regions of New Mexico (Wooten, 1908; 1915). New Mexico sheep populations have declined steadily since then, to about 400 000 in the late 1970's. Cattle numbers in the late 1970's were estimated at about 1.6 million, after several periods of decline in numbers (Schickedanz, 1980). There are data to indicate that actual grazing pressure has decreased considerably since the turn of the century, particularly on public lands (Branson, 1985).

Expectations of quick profit from exploiting the free and open ranges of the southwest fueled this 'cattle rush' and within a decade of its beginning, range degradation (i.e. depletion of palatable grass and forb production) was clearly underway (Bentley, 1898; Hastings and Turner, 1965; Wooten, 1908; 1915). Several accounts from that period confirm that since the late 1800's a number of changes in vegetation cover and soil erosion rates have occurred across the southwest, causing Hastings and Turner (1965) to conclude that unprecedented increases in grazing pressures, in combination with climatic factors (i.e. shifts in the intensity of rainfall events which will be discussed later; Cooke and Reeves, 1976; Leopold, 1951a) initiated the evolution of a 'new' vegetation assemblage that is still developing and expanding its range.

Fire

Early twentieth-century observers (Griffiths, 1910; Thornber, 1910) expressed the opinion that fire had previously checked the expansion of mesquite from drainageways to the intervening uplands. They predicted continued invasion and increase of mesquite on the uplands if heavy grazing continued to reduce fuel loads and fire frequency. Subsequent debate on the role of fire in excluding shrubs from grasslands prior to the 1880's has been concerned with two issues: (1) the frequency and extent of pre-1880 grassland fires; and (2) the effect of fires on shrubs.

Bahre (1985) and Humphrey (1958) concluded from newspaper accounts and several entries in traveler's journals that fires were larger and more frequent prior to 1882 than afterwards, when heavy grazing reduced fuel loads. Hastings and Turner (1965), however, found little evidence of widespread grassland fires in the earlier historical period. Fires are currently so uncommon in the mesquite and creosotebush shrublands of southern New Mexico and southeastern Arizona that data on fire frequency and extent are almost nonexistent.

Climate and Erosion

Cooke and Reeves (1976), Hastings and Turner (1965), and others have concluded that a combination of factors were responsible for increased arroyo cutting near the turn of the century (see Bryan, 1928; Duce, 1918). In addition to a rapid influx of grazing cattle and sheep to Texas, New Mexico, and Arizona during the 1880's, precipitation records reviewed by Cooke and Reeves (1976) and Leopold (1951a) indicate no detectable trends in total precipitation, but a higher frequency of intense storm events and fewer light rains for the period 1870 to about 1900 (Figure 4). However, Sellers (1960) found evidence for a decreasing trend in total

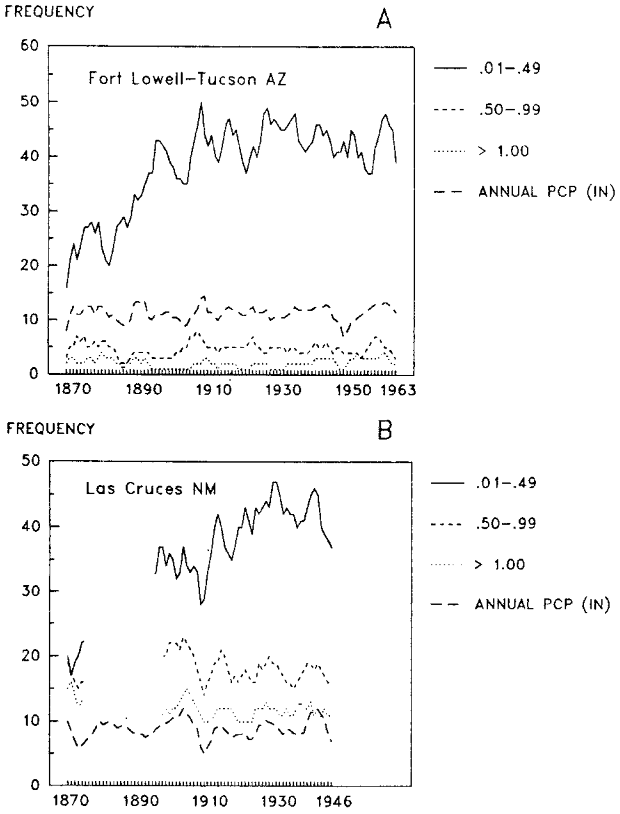

Fig. 4. Precipitation records for (A) Fort Lowell-Tucson, AZ. (redrawn from Cooke and Reeves, 1976), and (B) Las Cruces, N.M. (redrawn from Leopold, 1951a) showing changes in the frequency of rainfall intensities versus total annual precipitation (shown in inches for convenience of presentation).

annual precipitation in the records of 18 stations in Arizona and southeastern New Mexico for the period 1898 to 1959. The decreasing trend he noted was due primarily to declining cool season (November to April) precipitation.

Light rains tend to recharge surface soil moisture and thus favor the shallow-rooted grasses, whereas heavy rains which produce more runoff are less effective in soil moisture recharge on uplands. Heavy rains also recharge soil moisture in deep layers where it is unavailable to grasses but vital to the survival of deep-rooted shrubs during drought. The combined effect of increased grazing pressures and lack of light rains, or changes in the seasonality of rains, could have reduced vegetation cover more than increased grazing or altered precipitation alone, resulting in increased susceptibility to surface erosion by either water or wind. Decreased perennial grass cover is a key factor favoring not only soil erosion, but shrub invasion as well. In some areas, surface soil erosion may expose buried horizons more favorable for shrub establishment.

4. Shrub Establishment and Persistence

Both mesquite and creosotebush reproduce largely by seed (Parker and Martin, 1952; Valentine and Gerard, 1968). Vegetative reproduction by splitting of the root crown (Vasek, 1980) or sprouting of buried stems and exposed roots (Wallace and Romney, 1972) may contribute slightly to local population increase but is unimportant in the invasion of new areas. Mesquite stems buried by wind-blown sand are capable of sprouting new shoots and roots, leading to the formation of coppice dunes around these shrubs (Hennessy *et al.*, 1985; Gibbens *et al.*, 1983; Wright, 1982; Wright and Honea, 1986).

Newly established creosotebush may begin to produce seed after 5–13 years, and seed production becomes abundant by 5 years thereafter (Chew and Chew, 1965; Valentine and Gerard, 1968). Several factors that reduce seed production and viability may be important in setting distributional limits for creosotebush. Failure to produce viable seed has been attributed to periods of extremely cold winter temperatures (Beatley, 1974a; Shreve, 1940; Valentine and Gerard, 1968). Excessive soil moisture damages flowers (Beatley, 1974a; Dalton, 1961) and reduces seed production (Valentine and Gerard, 1968), possibly limiting the expansion of creosotebush into areas with higher precipitation (Beatley, 1974a). At the local scale, isolated individuals in a grassland matrix produce fewer seeds than individuals surrounded by other shrubs because isolated plants are frequently clipped by rodents and rabbits and trampled by larger animals, stimulating vegetative growth but reducing seed production (Valentine and Gerard, 1968; Wallace and Romney, 1972).

Creosotebush has no apparent specialized adaptations for seed dispersal, and few seedlings are found beyond about 100 m from the parent plant (Chew and Chew, 1965; Valentine and Gerard, 1968). Sheetwash, strong winds, and collection and caching of seeds by small rodents are responsible for most of this short-distance dispersal. Dispersal over longer distances might occur by the mud-caked hooves of cattle or antelope, or by birds, including those which prey upon seed-eating rodents (Hunziker *et al.*, 1977).

Successful creosotebush seedling establishment is apparently rare and episodic, perhaps requiring an unusual sequence of environmental conditions (Barbour, 1969; Wallace and Romney, 1972). Intense rainfall events promote successful seed germination by leaching the fruits (Barbour, 1968) and burying them in accumulations of soil and plant debris resulting from sheetflood erosion and deposition. Soil temperature requirements may largely restrict germination to the fall (Barbour, 1968; Rivera and Freeman, 1979). Most field observations of abundant germination have followed heavy fall rains (Beatley, 1974b; Rivera and Freeman, 1979; Sheps, 1973; Went and Westergaard, 1949).

Although mature creosotebush are capable of surviving long periods of very low soil and tissue water potential (Barbour *et al.*, 1977), seedlings may be killed by much shorter periods of drought (Clark *et al.*, 1974; Musick, 1977). Therefore, survival of seedlings probably depends on development of a deep and extensive root system and initiation of physiological tolerance mechanisms before the first severe drought is experienced. Early root growth requires warm soil temperatures (Barbour, 1968; Wallace and Romney, 1972). First-year survival would thus be favored by mild temperatures and frequent rainfall in the winter and spring after germination. Mature creosotebush are extremely long-lived, in some cases attaining an age of several hundred to several thousand years (Vasek, 1980).

In southern Arizona and New Mexico, mesquite sheds its beanlike fruits in late spring and early summer near the beginning of the summer rainy season (Glendening and Paulsen, 1955). Fruit production is usually abundant but may be reduced in some years by drought (Parker and Martin, 1952) or severe winter freezes (Felger, 1977). Domestic livestock, rodents, and flowing water are the major agents of dispersal (Glendening and Paulsen, 1955). Cattle have been especially important in dispersal because they eat large quantities of fruit, travel long distances, and deposit large numbers of intact seeds in their dung. Germinability is enhanced by passage through the digestive tract, and the seed is provided with a moist, nutrient-rich microenvironment for germination and early growth (Parker and Martin, 1952; Glendening and Paulsen, 1955).

Seedling mortality is very high in the first year, with the principal causes being drought (Bogusch, 1951; Paulsen, 1950) and predation by rabbits (Parker and Martin, 1952) and rodents (Paulsen, 1950). The age structure of natural populations suggests that favorable years for establishment occur only occasionally (Fisher, 1977; Scifres *et al.*, 1971), but probably not so rarely as for creosotebush. Mortality drops sharply after the first year as the plants become more resistant to drought and capable of resprouting if the aboveground parts are destroyed or killed by grazing, severe winter freezes, or fire (Glendening and Paulsen, 1955; Parker and Martin, 1952). Excessively frequent freezing damage may be important in setting the northern distributional limits of mesquite (Bogusch, 1951).

Depletion of grass cover greatly enhances establishment of mesquite (Glendening and Paulsen, 1955) and probably also creosotebush. Local episodes of mesquite invasion or establishment often follow drought-induced reductions in grass cover and yield (Herbel *et al.*, 1972; Scifres *et al.*, 1971). Branscomb (1958), Wright (1982), York and Dic-Peddie (1969), Hastings and Turner (1965), and others have suggested that the combination of drought and grazing may promote shrub invasion by reducing grass cover and exposing sites for establishment of shrubs that will in turn respond more vigorously when the supply of moisture improves. This is particularly true for mesquite, which rapidly forms deep taproots and long lateral roots near the surface (Hennessy *et al.*, 1983; Parker and Martin, 1952).

The rate of shrub invasion is variable across sites and years, but in general, complete dominance of an area may occur within a few decades. Hennessy *et al.* (1983) observed complete conversion from grassland to mesquite dominance within 45 years. Wright and Van Dyne (1981) used a population model to show that mesquite could replace a grassland stand within 30 years. Beck and Tober (1985) found that creosotebush reestablishment 22 years after shrub removal and grazing exclosure was generally less than 10% of original densities. Chew and Chew (1965) reconstructed the population history of a creosotebush stand in southeastern Arizona and estimated that density was low for the first 30 years after invasion (beginning in 1893), but then increased over the next 25 years to near the present high level.

Once shrub invasion has begun, reversing the process naturally or through human intervention is difficult or impossible. A number of studies have shown that mesquite cover will continue to increase even with protection from grazing (Brown, 1950; Norris, 1950), prescribed fire (Cable and Martin, 1973) or herbicides (Fisher, 1977). Results are similar for creosotebush (Cox *et al.*, 1986), but reestablishment may be slower and more erratic than for mesquite (Beck and Tober 1985).

In summary, our review of the life history characteristics of creosotebush and mesquite reveals that:

- adult survivorship is uniformly high, therefore the progress of invasion and subsequent density increase is determined largely by the degree of success in reproductive processes (seed production, dispersal and germination, and seedling establishment);
- seedling establishment is especially rare and episodic for creosotebush but less so for mesquite;
- depletion of grass cover by drought and grazing greatly increases susceptibility to invasion; and
- post-invasion increase of mesquite may proceed rapidly, even in the absence of grazing, while creosotebush invasion and increase may require favorable seasonal moisture regimes that occur infrequently.

5. Positive Feedback Mechanisms

The recent historical conversion of southwestern grasslands to shrublands is best viewed as resulting from disruption of a quasi-stable equilibrium (Fisher, 1977; Parker and Martin, 1952; Schlesinger *et al.*, 1990). Once the balance was tipped even temporarily in favor of shrub invasion, several positive feedback mechanisms functioned to perpetuate the process even though the initial triggering factors may have returned to their original state. There is strong evidence for the operation of positive feedback mechanisms involving edaphic and biotic factors, and at least the possibility of positive climatic feedbacks.

Edaphic

In creosotebush stands, exposure of shrub root crowns and carbonate crusts on rocks often provides evidence of 2 to 5 cm of soil loss by sheetflood erosion. Cooperrider and Hendricks (1937) and Gardner (1951) observed that much of the surface soils along the Rio Grande corridor from central to southern New Mexico had probably been lost in this manner, implying that reestablishment of perennial grasses had become an impossibility in many areas (see also York and Dick-Peddie, 1969).

Dune formation in sandy areas that have become dominated by mesquite has increased substantially since the turn of the century (e.g., Buffington and Herbel, 1965; Gile and Grossman, 1979). Gibbens *et al.* (1983), in comparing permanent transect data for the Jornada Experimental Range from 1935 and 1980, found that the depth of dunes around mesquite shrubs had increased in some areas by more than 80 cm, deflation between dunes had lowered soil levels by as much as 64.6 cm, and the total areal coverage of dunes had increased almost six-fold. Calculated gross erosion rates were greater than 50 tonnes/ha/yr.

The long-term consequence of aeolian processes in mesquite dune areas includes the loss of surface soil horizons in the interdune areas (Wright and Honea, 1986), alteration in soil texture on (coarse) *vs* off (fine) the dunes (Hennessy *et al.*, 1985; Paulsen, 1953), and enrichment of dune soils in organic matter, total nitrogen, and other soluble salts (Barth and Klemmedson, 1978; Tiedemann and Klemmedson, 1973). Soil surface temperatures and evaporation rates were also found to be higher for interdune soils than for dune soils (Hennessy *et al.*, 1985), which may partially explain why interdune plant cover is often sparse in these areas. Others have suggested that lateral root formation by mesquite effectively depletes soil moisture for up to 25 m from the shrub, outcompeting perennial grasses and further contributing to their decline in cover (Parker and Martin, 1952). Perennial grass and forb cover inhibit aeolian transport of surface soils (Gould, 1982), but once herbaceous plants are lost, mesquite shrubs act as effective sand traps in these areas (e.g., Gile, 1966).

Together, these findings indicate that creosotebush and mesquite establishment generates conditions unfavorable for perennial grass growth. More important, the resulting edaphic conditions favor continued soil erosion and subsequent shrub establishment.

Fire

Fire in grasslands consumes the litter and aboveground standing foliage but rarely kills the buds and meristematic growth regions protected in rootcrowns or belowground rhizomes. Growth in the first few years after fire is often greater than before the fire, in part due to the release of nutrients previously sequestered in accumulated dead plant material (Vogl, 1974). Fire is partially effective in killing mesquite and creosotebush; some individuals are completely killed, some are damaged but survive, and others resprout from the rootcrown after their stems are consumed or killed (Fisher, 1947; Glendening and Paulsen, 1955; Reynolds and Bohning, 1956; Wright *et al.*, 1976; McLaughlin and Bowers, 1982).

The contrasting patterns of spatial arrangement of aboveground biomass in grasslands and shrublands result in different susceptibilities to fire ignition and spread. Aggregation of biomass in and under shrub canopies results in larger intercanopy gaps than in grassland. Only under exceptionally favorable conditions is the growth of ephemeral plants under and between shrubs sufficient for extensive fire spread in these shrublands (McLaughlin and Bowers, 1982). Grassland canopies are highly combustible; moisture is very low at the onset of the summer rainy season, when convective storms often produce frequent lightning but little precipitation, and the canopy is loosely arranged, finely divided, and relatively evenly dispersed with few large gaps (Vogl, 1974).

Our view is that fire was one factor acting in concert with several others to limit shrub invasion of pre-1880 grasslands. Even partial mortality is effective in limiting population growth, and repeated burning may have kept individual shrubs small and thus more susceptible to other causes of mortality.

Climatic

Changes in vegetation composition, physiognomy, and spatial distribution may alter several components of the surface energy budget and thereby influence climate on both the local and regional scales (Berkofsky, 1976; Charney, 1975; Dickinson, 1983). Controversy has arisen from conflicting observations of the effect of desertification or land degradation on surface albedo, evapotranspiration, and surface temperature (Lockwood, 1983; Nicholson, 1988; Wendler and Eaton, 1983). Many of the conflicting observations could be reconciled and much controversy avoided by recognizing that desertification and land degradation are broad concepts encompassing a wide variety of vegetation and land surface changes. It cannot be assumed that the magnitude or even the direction of change in energy budget components observed for one pair of pre- and post-degradation surfaces will apply to all land surface changes to which the terms desertification or land degradation could be applied. For example, Otterman (1974; 1975) and Jackson and Idso (1975) arrived at strongly contrasting views on the effect of land degradation on surface temperature largely because the pre-degradation 'vegetated' surfaces examined by each were extremely different: i.e. an irrigated wheat crop by Jackson and Idso versus a sparse cover of non-transpiring leafless stems by Otterman.

Most studies of land degradation effects on surface energy budgets have been based on examples of substantial or complete denudation (i.e. removal of vegetation). Shrublands in the southwestern U.S. are not denuded; they may have either more or less vegetation than relictual grasslands on comparable sites depending on the measure of vegetation amount applied (e.g., canopy cover, aboveground biomass) and other factors (Warren and Hutchinson, 1984; Webb *et al.*, 1983). Shrubland encroachment has resulted in changes in small-scale spatial distribution of plants, in canopy architecture, and in seasonal patterns of vegetative activity. These changes may be as important as the difference in vegetation amount in determining the effect on surface energy budgets of a grassland-to-shrubland conversion.

Albedo change resulting from denudation is highly variable, but increases equaling or exceeding 0.2 are not uncommon (Nicholson, 1988; Otterman, 1981). The few data available for southwestern grassland and shrubland suggest that the albedo change resulting from shrubland encroachment has been slight. We obtained daily shortwave radiation fluxes continuously for ten months at a creosotebush site and a nearby grassland site on similar soils in southern New Mexico. Mean daily albedo was 0.213 for the creosotebush site and 0.208 for the grassland site (not significantly different at $p = 0.05$). A mesquite and snakeweed dominated site in southern New Mexico, similarly monitored for another study (Breed *et al.*, 1985), had a mean daily albedo of 0.19. Bryson *et al.* (1970) reported albedo values of 0.20 for creosotebush communities 0.26 to 0.27 for mesquite, and 0.20 to 0.25 for various grassland communities in southern New Mexico.

Because almost all of the precipitation falling in an arid region ultimately leaves the system by evapotranspiration (Evans and Thames, 1981), shrubland encroachment has probably had little effect on annual regional evapotranspiration as a fraction of rainfall. Differences in vegetative phenology of shrubs versus grasses may have somewhat modified the temporal pattern of evapotranspiration, but thirty percent or more of evapotranspiration in these regions is by direct evaporation from soil and thus not subject to physiological control (Evans *et al.*, 1981; Schlesinger *et al.*, 1987). Surface runoff may have increased on some landforms and soil types, but the decreases in evapotranspiration from uplands are probably largely compensated by enhancement of water supply and evapotranspiration in drainage channels and enclosed basins.

Bryson *et al.* (1970) used a modelling approach (see Lettau, 1969) to estimate the annual course of surface temperature and heat budget components for mesquite dunelands and adjacent grasslands. They estimated that grassland surface temperature would be 1° to 2.5° warmer than mesquite duneland and attributed most of the temperature difference to the lower aerodynamic surface roughness of the grassland.

Although measurements of the impact of shrubland encroachment on surface energy budgets are scarce, we suggest that effects have been much smaller than in those cases of land degradation where substantial denudation has taken place.

Another difficulty in assessing the potential effects of shrubland encroachment on the climate of the southwestern U.S. is the complexity of mesoscale circulation patterns and their controls in this physiographically heterogeneous region. Convective precipitation in this region is influenced not only by surface properties of the lowlands where shrubland has replaced grassland, but also by such factors as differential heating of mountain slopes versus lowlands, orographic lifting and downslope flow resulting from regional airflow across mountains, and by evapotranspiration from the woodlands and forests of the higher mountain slopes (e.g., Houghton, 1979). Addressing the problem of climatic effects of shrubland encroachment will require advancements in mesoscale climate models and better long-term datasets from systematically located monitoring stations.

Biotic

Overall, invasion of grasslands by creosotebush or mesquite results in distinct changes in the species composition, physiognomy, abundance, and spatial distribution of vegetative cover. By definition, the proportion of woody species will increase with shrub invasion. More important is the decline in grass cover that can be supported once shrubs become dominant, and the localization of forbs and other grasses near shrubs (e.g., Hennessy *et al.*, 1983; Parker and Martin, 1952; Wright and Honea, 1986). Thus, although total plant biomass and cover may remain about the same or even increase with shrub invasion the spatial distribution of plants is changed significantly.

Localization of forb and remaining grass cover under mesquite or on dunes formed by mesquite plants, leaving barren interdune areas, is characteristic of mesquite dominated areas in full development (Wright, 1982). Factors contributing to this condition include alteration in local physical factors discussed above (i.e. higher surface temperatures and evaporation rates in interdune areas), and higher-order effects of spatial heterogeneity in vegetation distribution on biogeochemical cycling (see Schlesinger *et al.*, 1990; Whitford *et al.* 1987).

Wright and Honea (1986) reported increased soil nitrogen in coppice dune soils. Similar findings have been reported for other aridland ecosystems where nutrient concentrations and biogeochemical cycling rates were greater under shrubs than in inter-shrub gaps (Skujins, 1981; Crawford and Gosz, 1986; Whitford *et al.*, 1987). By concentrating nutrients around shrubs, recovery of perennial grasses and other vegetation in intershrub gaps becomes less probable, perpetuating a shrubland system.

Other biotic feedbacks involved with shrubland invasion involve changes in the species composition and food habits of the consumer community. Several reports document increased small rodent and rabbit populations in mesquite and creosotebush areas (e.g., Buffington and Herbel, 1965; Norris, 1950). Some authors contend that grazing by rodents and rabbits can favor shrub invasion by decreasing grass cover, and by disseminating shrub seeds (e.g., Norris 1950). Studies using a series of fences to exclude combinations of cattle, rodents, rabbits, or all three, indicate that both creosotebush (Beck and Tober, 1985) and mesquite (Brown, 1950) invaded or reestablished themselves regardless of exclosure regime. However, exclosure studies generally find some improvement in grass cover with total exclusion of grazers compared to partial exclosures (see also Norris 1950).

6. Model of Shrub Invasion

Here we propose a model that synthesizes many of the factors reviewed above. Portions of this model have been presented elsewhere (e.g., Schlesinger *et al.*, 1990; Whitford *et al.*, 1987; Wright, 1982). In our model, we draw specific attention to: (1) the triggering of a sequence of changes in landscape structure by coincident biological (grazing) and physical factors (fire and climatic patterns); and (2) the perpetuation of these changes by positive feedbacks. We also address several factors affecting the spatial and temporal dynamics of landscape change by suggesting that effectively permanent change may occur episodically as a result of periodic or secular changes in climatic, biotic, or edaphic controls that coincide and exceed some critical threshold for shrub establishment.

Figure 5 summarizes the information reviewed in this paper. Establishment of

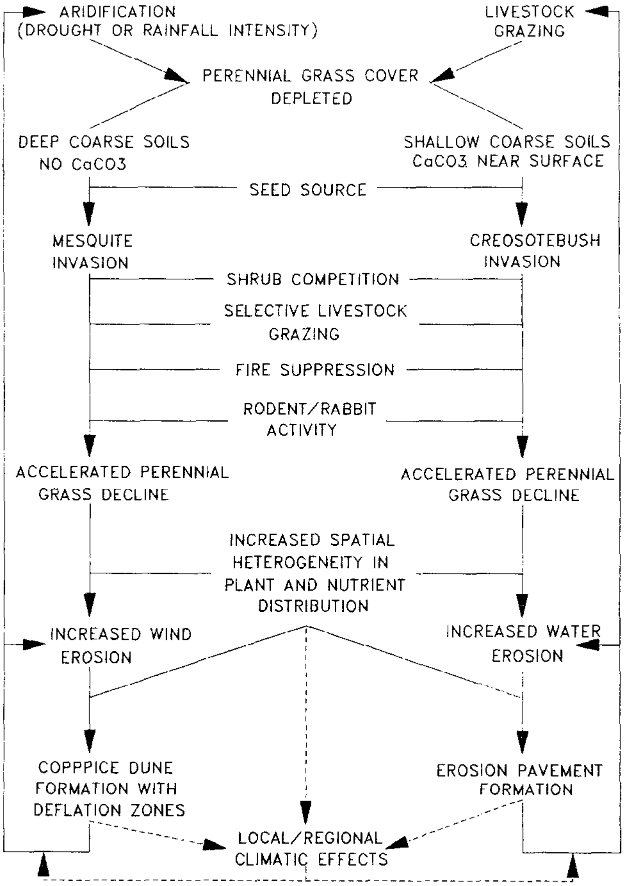

Fig. 5. Synthetic model of shrubland invasion for the American southwest based on creosotebush and mesquite life histories and the observed consequences of their dominance.

shrubs (i.e. creosotebush or mesquite) is favored by depletion of grass cover resulting from the combined effects of livestock grazing and sub-optimal precipitation amount or effective moisture supply (e.g., greater runoff and less infiltration with high intensity rains). These conditions also reduce the probability of fires because of a lack of fuels.

The rate of seed introduction into areas with appropriate soil conditions limits invasion. Cattle, rodents, and other animals serve as important dispersal agents which supply seeds to new areas and permit the establishment of pioneer shrubs. In the absence of fire, once pioneer shrubs become established and mature, density can increase through periodic establishment of their progeny. A number of factors may then combine to accelerate the decline in grass cover, which favors continued shrub invasion. For example, competition for soil moisture and nutrients between grasses and shrubs will increase. Also, since shrubs are unpalatable to livestock and small grazers, selective grazing on the remaining grasses and forbs will deplete them further. Decreased herbaceous cover permits increased surface soil erosion, primarily by wind on soils favored by mesquite, and by water on creosotebush soils. The result is a significant alteration in landscape structure, such that conditions favorable for plant growth (e.g., soil moisture, surface temperature, nutrient supply) become localized in the vicinity of shrubs. Intershrub soils may become less favorable for plant growth through continued erosion and/or shrub invasion. Local and regional climatic effects of these changes in vegetation are possible, but as discussed earlier, have not been conclusively demonstrated by available evidence.

Important features of the spatial and temporal dynamics of shrub invasion are conceptualized in Figure 6. Shrub dominance is shown to increase in a 'ratchet-pulse' pattern; that is, pioneers may invade appropriate facets of the landscape mosaic when combined climatic-biotic conditions in those areas allow. Once established, shrubs are long-lived and do not relinquish their dominance. Because of spatial heterogeneity in edaphic factors (e.g., depth to caliche, drainage), the necessary climatic/biotic conditions may not be the same for all landscape facets, but these edaphic conditions may change through time (e.g., due to surface soil erosion), as may the climatic or biotic factors (e.g., changes in precipitation amount, frequency, or intensity). In this way, areas not invasable at one point in time, may become so later on as a result of periodic or secular shifts in climatic/biotic controls, or through the feedbacks illustrated in Figure 5 related to initial shrub establishment.

Until recently, explanations of rangeland response to grazing pressure have been based on a conceptual model of continuous transition along a continuum from climax vegetation in excellent condition to early successional vegetation in poor condition (e.g. Dyksterhuis, 1958). In this 'range succession' model (see Westoby *et al.*, 1989) the position of the vegetation along this continuum is viewed as resulting from an equilibrium between opposing processes; drought and grazing pressure push the system towards poorer condition and earlier successional stages, while above-average rainfall and the natural processes of succession tend to improve

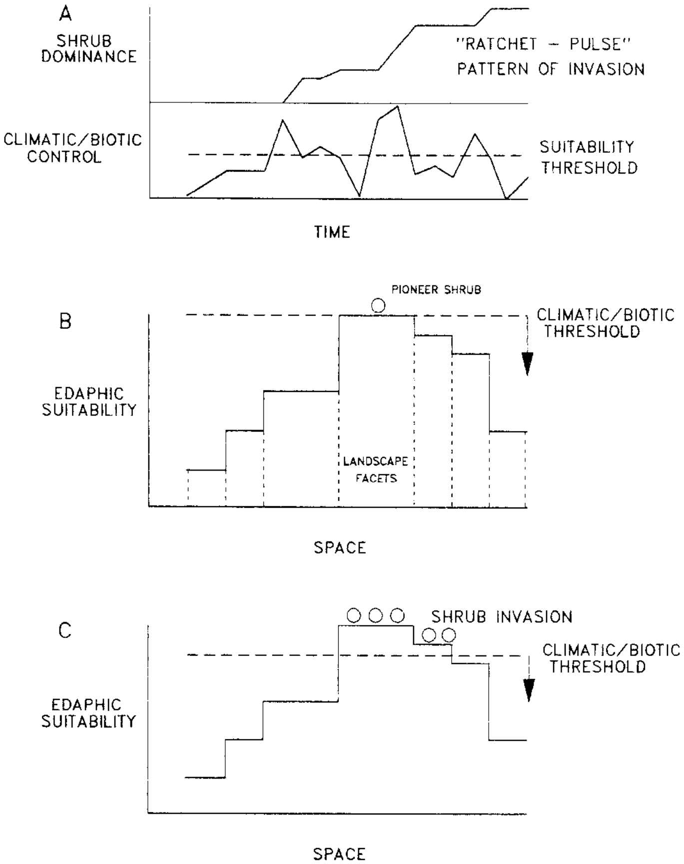

Fig. 6. Schematic representation of spatial and temporal dynamics in edaphic, climatic, and biotic controls affecting shrubland invasion.

range condition and drive the system towards the state of successional climax. The process of shrub encroachment of grasslands in the southwestern U.S. seems to be better explained by an alternative 'state-and-transition' model in which rangeland dynamics are described by a set of discrete states connected by a set of discrete transitions triggered by natural events or management actions (Walker *et al.*, 1981; Westoby *et al.*, 1989). State-and-transition systems are characterized by multiple alternative stable states, discontinuous and sometimes irreversible transitions, and non-equilibrium communities (Westoby *et al.*, 1989). These characteristics of state-and-transition systems reflect the importance of positive feedback processes and threshold effects like those contained in Figures 5 and 6. For example, the ratchet-pulse aspects of our model describe a state-and transition sequence whereby landscape facets periodically enter transition states.

Vegetation response to climate change is often modeled as a continuous and strictly deterministic process. Although this may be a suitable model for change at the global scale and for either very long or very short temporal scales, a state-and-transition model might be more appropriate for many cases of vegetation response at regional to local scales and for intermediate time scales (i.e. 10^1–10^3 yr).

7. Future Trends

The areal extent of shrubland encroachment described for the southwest is enormous, equivalent to the total area of the New England states plus New York and Pennsylvania, thus rivaling in expanse the deforestation that occurred in the New England states in the eighteenth century. In New Mexico alone, the areal coverage of mesquite plus creosotebush nearly equals the size of Pennsylvania. But what are we to expect in the next several decades? Will creosotebush and mesquite expand their range, or will their distribution be limited by climatic, edaphic, or biotic factors that have, for the last century, been ineffective in prohibiting shrub invasion? And what is likely to happen in those areas already invaded by creosotebush and mesquite? Will their dominance increase, or could more prudent management practices coupled with favorable climatic conditions result in recovery of the perennial grass cover?

Soil factors appear to limit the potential of creosotebush to completely occupy its geographical range. Soils capable of supporting creosotebush are generally calcareous throughout the profile and gravelly, while soils that are fine-textured or lack near-surface carbonate horizons tend to be devoid of creosotebush (Hallmark and Allen, 1975; Musick, 1978), but may support mesquite.

To estimate the total potential coverage of creosotebush in New Mexico, we performed a coarse scale analysis based upon the areal distribution of soil associations classified as to their suitability for creosotebush establishment. The major soil associations for the warm desertic region of New Mexico (mapped at 1 : 1 million scale, see Maker *et al.*, 1974) were categorized on the basis of carbonate horizons and texture as either mostly suitable or mostly unsuitable for creosotebush. A third category consists of soil associations which are marginally suitable or are mixtures of suitable and unsuitable soil series. We estimate that about half of this marginal and mixed category is capable of supporting creosotebush (Table II).

Comparison of the soil suitability map (Figure 3) with the creosotebush-tarbush distribution map from the countywide surveys (Garrison and McDaniel, 1982) revealed considerable agreement in spatial distribution. We estimate that of the 3.7 million ha of creosotebush-tarbush, at least 80% (2.9 million ha) contains creosotebush. This is very near the total area of mostly suitable and marginally suitable soils (3.1 million ha; Table II), suggesting that creosotebush has already invaded most of the suitable soils within its geographical range in New Mexico.

Further expansion in the range of creosotebush could occur if unsuitable soils become more suitable. Unsuitable soils with calcareous subsoils could become more suitable if the subsoil was exposed by erosion (sensu ratchet-pulse model; Figure 6). Creosotebush might also extend its range into adjacent, less xeric areas where suitable soils are present. Although most suitable soils are confined to the warm desertic region, some are also found in the southern parts of the central plains. This latter area is cooler and receives more rainfall than the warm desertic region where creosotebush is abundant and only a slight climatic change might be sufficient to open up large areas to potential creosotebush invasion.

We have not attempted a similar analysis of potential mesquite expansion based on soil properties because this shrub grows on a wide range of soil types (Parker and Martin, 1952). However, it is important to note that of the 7.58 million ha of mesquite in New Mexico, approximately 3.32 million ha are on central and southern high plains soils (Table I and Figure 3; based on data reported in Garrison and McDaniel, 1982, for mesquite distribution in counties with predominately these soils). Expansion in the range of mesquite on these soils has been underway and continues. As with creosotebush, the ability of mesquite to gain increasing dominance in these areas is probably limited by soil factors and by seed source. We have seen no estimates of potential range extension for mesquite, but are acutely aware of its potential to dominate a broader expanse in the southern and eastern plains of New Mexico and much of western Texas.

8. Summary

The economic impacts of shrub invasion are significant at the local and regional scale; the ecological impacts at these scales is not well understood. As this paper reveals, the factors that have contributed to shrub encroachment are complex because they are highly interactive. It may very well be that the increase in shrub dominance we have seen over the last century was triggered by coincident climatic conditions and overgrazing at the turn of the century, followed by periods of favorable conditions for shrub establishment. If so, rangeland managers must take a longer view when considering the implications of their practices. Moreover, decisions must be based upon a firmer understanding of landscapes rather than individual species, and we must improve our responsiveness to short-term and long-term patterns in climate. By improving our understanding of what has happened in the American southwest, we may realize that this landscape is responding to climate change, providing us with valuable clues to how regional landscapes might be altered by the patterns in climate change projected for the next century.

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