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HAVE SOUTHERN TEXAS SAVANNAS BEEN CONVERTED TO WOODLANDS IN RECENT HISTORY?

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Quantitative and historical assessments suggest that woody-plant abundance has increased substantially in arid and semiarid grasslands over the last 50 to 300 years in many parts of the world, including Africa (Barnes 1979; Wickens and Whyte 1979; van Vegten 1983), India (Singh and Joshi 1979), Australia (J. Walker and Gillison 1982), and South America (Schofield and Bucher 1986; Bucher 1987). This phenomenon has been widespread in North American grasslands as well (Buffington and Herbel 1965; Blackburn and Tueller 1970; Smeins 1983; Hobbs and Mooney 1986). Although descriptions of the physiognomic conversion of grassland to shrub land or woodland are abundant, little is known of mechanisms, rates, or dynamics of the process. Simulations by Emanuel et al. (1985*a,b*) indicate that grasslands of arid and semiarid regions will become increasingly susceptible to woody-plant encroachment in response to anticipated global climatic changes. Thus, interactions between grasses and woody plants in a successional context may become increasingly important.

The Rio Grande Plains of southern Texas and northeastern Mexico offer some distinct examples of processes involved in the conversion of grasslands to woodlands. The natural vegetation of this region has been classified as a *Prosopis-Acacia-Andropogon-Setaria* savanna (Küchler 1964). However, present-day vegetation is subtropical thorny woodland. A component of the much larger Tamaulipan Biotic Province (Dice 1943), this thorn-scrub vegetation is similar to that of the Caribbean, Sinaloan, and San Lucan biotic provinces (D. Brown 1982). In many instances, it is believed that these vegetational types have developed on areas of former grasslands. However, the argument that the increased prominence of shrub lands and woodlands has contributed to the demise of prairies and savannas in southern Texas is controversial (Malin 1953). Most evidence is from indirect, historical sources (Bogusch 1952; Inglis 1964), substantiated in a limited analytic context (Johnston 1963).

Mechanisms of the conversion process from grassland to shrub land in the eastern Rio Grande Plains have recently been described elsewhere (Archer et al. 1988). In that study, vegetation consisted of discrete, circular clusters of woody plants scattered throughout an herbaceous matrix. The clusters, ranging from 1 m to 40 m in diameter and containing 1 to 15 woody species, were chronosequences

(i.e., time-ordered vegetational states; Barbour et al. 1987) organized around a lone mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) nucleus. As *Prosopis* invaded and developed in the herbaceous zone, new clusters formed. At the same time, existing clusters expanded as new species were added and canopies of established plants developed. If this process continues, clusters will eventually coalesce to form a continuous canopy cover. The present savanna woodlands were thus hypothesized to represent an intermediate stage in the physiognomic conversion of a grassland to a woodland.

In an effort to quantify the rates and dynamics of this process, data summarized previously (Archer et al. 1988) were used to simulate cluster growth and development. Model-derived estimates of the relationships between cluster size and age were then applied to field data on cluster size distributions to estimate the ages of woody-plant assemblages on the present landscape. Cluster age-class distributions were then used to reconstruct the history of stand development and to estimate when woody-plant invasion may have begun.

SITE DESCRIPTION

Field data used in the model are from studies conducted at the Texas Agricultural Experiment Station, La Copita Research Area, near Alice, Texas (27°40' N; 98°12' W), in the Rio Grande Plains of the Tamaulipan Biotic Province (Dice 1943). Contemporary vegetation of the region has been described by Davis and Spicer (1965). Vegetation is a savanna woodland with discrete clusters of woody plants organized beneath *Prosopis*. The site has been grazed by cattle since the late 1800s, and woody-plant cover has increased 23% since 1941 (Archer et al. 1988). Herbaceous vegetation between shrub clumps is dominated by the C₄ grasses *Paspalum setaceum*, *Setaria geniculata*, *Bouteloua rigidisetata*, and *Chloris cucullata* (plant nomenclature follows Correll and Johnston 1979). The climate is subtropical with warm winters and hot summers. Mean annual rainfall is 68 cm with maxima in May and September. Mean annual temperature is 22.4°C with a growing season of 289 days. Soils at the upland study site are fine, sandy loams derived from sandstones. Elevation ranges from 75 to 90 m.

MODEL DEVELOPMENT

To quantify the growth of individual clusters, I used aerial photographs (approximately 1:20,000) from 1941, 1960, and 1983 (obtained from a previous study; Archer et al. 1988). Growth rates were observed to vary with precipitation and cluster size (table 1). The period from 1941 to 1960 was characterized by drought, whereas the period from 1960 to 1983 was typified by normal to above-normal rainfall (fig. 1). These periods are subsequently referred to as "dry" and "wet." To account for differences in the rates of cluster enlargement resulting from differences in absolute size, relative growth rates (RGR; Hunt 1978) were calculated:

$$\text{RGR} = (\ln S_2 - \ln S_1) / (t_2 - t_1), \quad (1)$$

where S_1 is cluster size (m²) at time t_1 , and S_2 is cluster size at time t_2 .

TABLE 1
RELATIVE GROWTH RATES (RGR, EQ. 1) OF
PROSOPIS-MIXED-SHRUB CLUSTERS IN
THE RIO GRANDE PLAINS, TEXAS

CLUSTER SIZE (m ²)	RELATIVE GROWTH RATE (m ² m ⁻² y ⁻¹)	
	Dry*	Wet†
<100	0.10	0.16
100-400	0.01	0.03
401-1000	0.01	0.02
>1000	-0.08	0.01

NOTE.—Rates were determined from aerial photographs (Archer et al. 1988).

* Growth during the 1941-1960 period characterized by a major drought.

† The period of normal to above-normal precipitation from 1960 to 1983 (fig. 1).

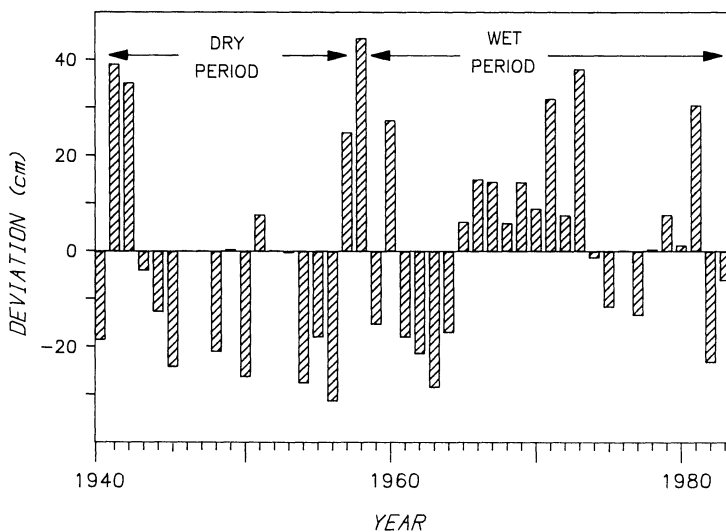


FIG. 1.—Deviation from the long-term mean annual precipitation (68 cm) at the study site near Alice, Texas, from 1940 to 1983. Growth rates of individual woody clusters were determined from aerial photographs (Archer et al. [1988] quantified sizes for 1941, 1960, and 1983). The period from 1941 to 1960 was characterized by drought, whereas the 1960-1983 period was one of normal to above-normal annual rainfall.

RGR of clusters less than 100 m² in canopy area were an order of magnitude greater than those of larger clusters. This was presumed to reflect rapid early growth of the *Prosopis* plant forming the center of the cluster. At later stages, cluster expansion resulted primarily from the recruitment and growth of individuals of other woody species around the perimeter of the *Prosopis* canopy. Subordinate species in clusters were smaller in stature than *Prosopis*, and many were

evergreens with low intrinsic growth rates. Thus, a decrease in RGR with increasing cluster size is reasonable.

During the wet period, the RGR of clusters smaller than 100 m² increased 60% relative to the dry period. The RGR of larger clusters also increased but remained an order of magnitude lower than small clusters. In the largest-size class, RGR was negative during the dry period. This decrease resulted from canopy reductions and/or mortality of individuals in clusters larger than 1000 m². Woody-plant mortality in this area during the drought period (Carter 1964) and ramifications for cluster growth and development (Archer et al. 1988) have been discussed elsewhere.

Cluster expansion was a function of the growth of individuals making up the cluster. The following equation from plant-growth analysis was thus used to express development over time (Hunt 1978):

$$S_2 = S_1 \exp[\text{RGR}(t_2 - t_1)], \quad (2)$$

where S_1 is the initial size of the cluster (m²) at time t_1 , and S_2 is the cluster size at a later time, t_2 . RGR was determined from equation (1) and varied with cluster size and precipitation (table 1).

Because cluster size (S , m²) was known, the basal diameter of the central *Prosopis* plant and species richness could also be predicted:

$$\text{Prosopis basal diameter (cm)} = (\ln S + 0.123)/0.17 \quad R^2 = 0.72, \quad (3)$$

and

$$\text{no. of species per cluster} = 9.74[1 - \exp(-0.116S)] \quad R^2 = 0.83. \quad (4)$$

The model was structured from the relationships in table 1 and equations (1)–(4). Precipitation (fig. 1) was varied stochastically between wet and dry periods. A series of rainfall scenarios was examined, in which the probability (P) of a wet period at a given time step ranged from 0.0 to 1.0. For each time step, the RGR selected for equation (2) depended on cluster size and on whether the period was wet or dry (table 1). For each precipitation scenario, the model output represents the mean of 30 runs.

The smallest distinguishable cluster on aerial photography used to estimate growth rates was about 4 m² (Archer et al. 1988). This represented a cluster nucleus composed of a *Prosopis* plant with a basal diameter of about 7 cm (eq. 3) and three understory species (eq. 4).

RESULTS

Maximum cluster growth occurred when $P(\text{wet}) = 1.0$ (i.e., every time step was a wet period) (fig. 2). Minimum growth occurred when $P(\text{wet}) = 0.0$ (i.e., every time step was a dry period). Two intermediate and more realistic rainfall regimes are also depicted. When dry periods were encountered, cluster size eventually became dynamically stable, oscillating around 1000 m². This occurred in 140 to 250 yr and was a consequence of shrinkage during dry years and low relative growth rates (RGR) in wet years among large-size classes (table 1).

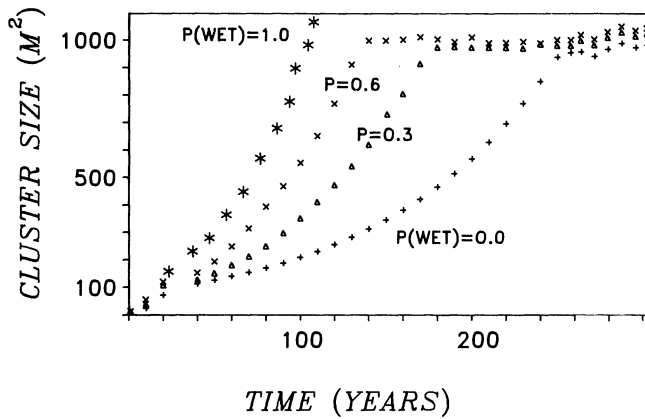


FIG. 2.—Growth of a woody cluster over time under a series of rainfall regimes. Growth began when clusters were 4 m² in area. When the probability of encountering a wet period, $P(\text{wet})$, was 1.0, growth at each time step (table 1) corresponded to that observed during the 1960–1983 period in figure 1; when $P(\text{wet}) = 0.0$, growth at each time step equaled that of the 1941–1960 period. Intermediate curves reflect cluster growth when $P(\text{wet})$ varied from 0.3 to 0.6. Each rainfall scenario represents the mean of 30 runs. Cluster age in real time can be determined by adding the age of the cluster nucleus in table 2.

TABLE 2

ESTIMATES OF RADIAL TRUNK GROWTH OF *PROSOPIS* DERIVED FROM CLUSTER SIZE (EQ. 3; FIG. 2)

$P(\text{wet})$	Radial Stem Growth (mm/yr)	Estimated Age (yr) of 7-cm Plant
0.0	0.8	44
0.3	1.2	30
0.6	1.6	24
1.0	1.9	18

NOTE.—Growth-rate estimates were used to project the age of the smallest clusters discernible (4 m²) by aerial photography (Archer et al. 1988). These clusters would have had a *Prosopis* plant of approximately 7 cm in basal diameter.

By estimating the size of the *Prosopis* plant in clusters, a second determination of cluster age was made. Basal diameter of the *Prosopis* in a cluster nucleus was 7 cm at the beginning of the simulation. When cluster growth became asymptotic in the $P(\text{wet}) < 1.0$ scenarios, *Prosopis* basal diameter was approximately 41 cm (eq. 3). Thus, *Prosopis* basal diameter increased by approximately 34 cm during the period of cluster expansion. Resulting basal growth rates of *Prosopis* plants, which represent a long-term average, were then used to estimate the age of the *Prosopis* plant in the cluster nucleus at the start of the simulation (table 2). Results suggest that *Prosopis* plants would be 18 to 44 yr of age when subordinate woody species begin appearing beneath them. Simulation time in figure 2 could thus be converted to real time by adjusting for the age of the *Prosopis*.

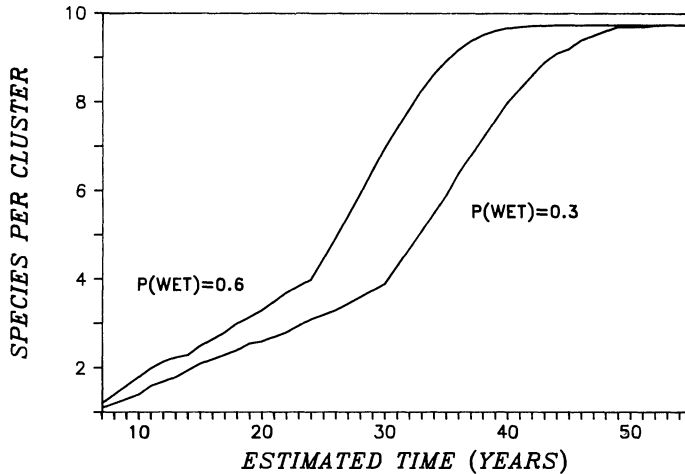


FIG. 3.—Changes in species richness (D) in developing clusters (fig. 2) under two rainfall regimes. $D = 1$ represents a lone *Prosopis* plant. Linear estimates of *Prosopis* basal growth (table 2) were used to determine richness in clusters smaller than 4 m^2 as follows: $D = 12.71[1 - \exp(-0.05M)]$, where M is *Prosopis* basal diameter in centimeters ($R^2 = 0.86$; Archer et al. 1988). For clusters larger than 4 m^2 , equation (4) was used.

As clusters develop, new species are added (fig. 3). *Opuntia lindheimeri* (Cactaceae) and *Zanthoxylum fagara* (Rutaceae) were typically the first woody species to occur beneath *Prosopis* (Archer et al. 1988). The frequency of occurrence (F) of these species with *Prosopis* plants having basal diameters of 3 cm and 6 cm or greater was 0.4 and 1.0, respectively. Assuming *Prosopis* radial trunk growth of 1.2 and 1.6 mm per yr (table 2), these subordinate species would have begun appearing 12 yr ($F = 0.4$) to 26 yr ($F = 1.0$) after invasion of the site by *Prosopis*. The next species to appear beneath *Prosopis*, with roughly equal probability, were *Celtis pallida* (Ulmaceae), *Condalia obovata* (Rhamnaceae), and *Diospyros texana* (Ebenaceae), which had a value of $F = 0.5$ when clusters were 8–11 m^2 in area (Archer et al. 1988), approximately 29–39 yr after *Prosopis* establishment (for $P(\text{wet}) = 0.6$ and 0.3, respectively). *Berberis trifoliolata* (Berberidaceae), *Schaefferia cuneifolia* (Celastraceae), and *Ziziphus obtusifolia* (Rhamnaceae) appeared with $F = 0.5$ when clusters were 20–22 m^2 or 36–45 yr old. Other species, such as *Lycium berlandieri* (Solanaceae), appeared with $F = 0.5$ only when clusters were larger than 55 m^2 or more than 45–52 yr of age.

Cluster and *Prosopis* size-age relationships from figure 2 and table 2 were applied to field surveys of cluster-size distributions (Archer et al. 1988) to estimate the age structure of woody assemblages on the present landscape. Regardless of the precipitation regime ($P(\text{wet}) = 0.3$ or 0.6), it appeared that only about 10% of the clusters were more than 100 yr old (fig. 4).

Estimates of *Prosopis* growth rates (table 2) were then applied to plants in clusters described in the earlier study (Archer et al. 1988). Results (fig. 5) were comparable to those observed for clusters (fig. 4) in that 89%–93% of the *Prosopis* plants were less than 100 yr old. Mean age was 35–44 yr and median age 25–30 yr

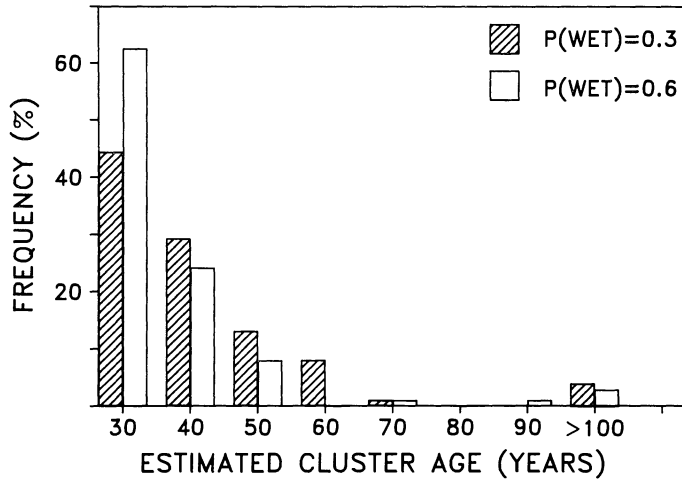


FIG. 4.—Age distribution of clusters derived from field size-class distribution data (Archer et al. 1988). According to model estimates, less than 10% of the clusters on the landscape were more than 100 yr of age in either rainfall regime.

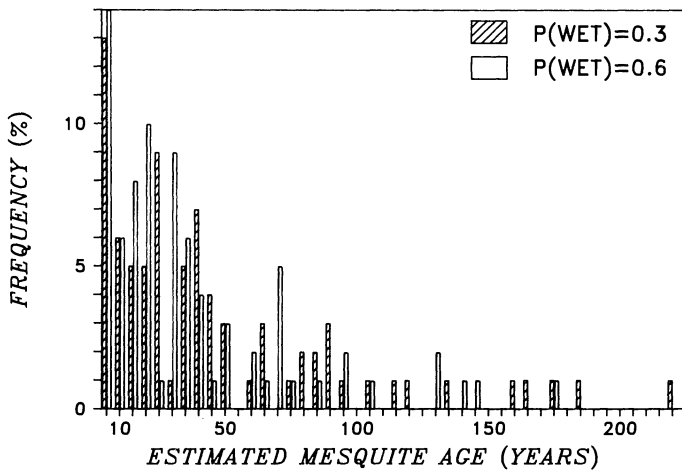


FIG. 5.—Age distribution of *Prosopis* plants in clusters, based on field measurements of basal diameter (Archer et al. 1988) and model-derived estimates of basal growth rates (table 2). Oldest plants found were 172 and 217 yr of age using $P(\text{wet}) = 0.6$ and 0.3 , respectively. However, 89% to 93% of the plants in their sample would be less than 100 yr old.

for $P(\text{wet}) = 0.6$ and 0.3 , respectively. Maximum ages for this arborescent legume were 172 and 217 yr for $P(\text{wet}) = 0.6$ and 0.3 , respectively. In about 25% of the clusters on the landscape, the *Prosopis* plant forming the nucleus had died (Archer et al. 1988). The basal diameter of these dead individuals was used to estimate their ages (table 3). Most of the plants (86%–91%) were less than 30 yr old at the time of death.

TABLE 3
 AGES OF DEAD *PROSOPIS* PLANTS FOUND IN FIELD
 SURVEYS OF CLUSTER CHRONOSEQUENCES
 (ARCHER ET AL. 1988) AND THE PERCENTAGE OF
 PLANTS IN EACH AGE CLASS

ESTIMATED AGE (YR)	PLANTS IN EACH AGE CLASS (%)	
	<i>P</i> (wet) = 0.3	<i>P</i> (wet) = 0.6
<10	27.3	39.4
20	39.4	45.5
30	18.2	6.1
40	6.1	3.0
50	3.0	3.0
60	3.0	3.0
70	3.0	0.0
>70	0.0	0.0

NOTE.—*N* = 33 plants. Estimates are based on growth rates given in table 2. Younger-age classes are probably underestimated because small plants decompose more quickly than large ones.

DISCUSSION

Model Evaluation

Although age-size relationships are often misleading (Harper 1977), the crude estimates of age structure generated by this model represent a first approximation of the population biology of woody plants for which there are no demographic data. False rings and the shrub growth form of woody plants in this subtropical climate make dating by ring-count methods unreliable (Fritts 1976). Quantitative validation of the model would require measuring cluster growth on another landscape over time. To date, that has not been possible.

Validity of the model can be evaluated qualitatively as follows. (1) The model predicted that most *Prosopis* plants and clusters on the present landscape have appeared since the late 1800s. This is consistent with historical observations. (2) Aerial photographs indicate an increase in mean woody-plant cover from 13% in 1941 to 36% in 1983; a significant shift in the size-class distribution to a higher proportion of larger clusters; and an increase in mean cluster size from 494 m² to 717 m² (Archer et al. 1988). Thus, the development of woody communities and clusters has been rapid and substantial over the past 50 yr. (3) Although no data were found for basal growth of *Prosopis* at upland sites in southern Texas, model estimates of *Prosopis* trunk growth (table 2) compare favorably with field measurements on *Prosopis* in other systems. In central Texas, where precipitation is higher and soils better developed, Haas (1970) recorded radial stem growth of 4 mm per yr over one growing season. Measurements of plants representing an array of sizes at a Rio Grande Plains lowland site in southern Texas averaged (\pm SE) over a 5-yr period were 1.9 mm \pm 0.9 mm per yr (R. S. Vora and J. F. Messerly, unpubl. data). Juvenile *Prosopis* in southern Arizona desert grassland had radial-stem growth rates of 1.3–2.5 mm per yr (Glendening and Paulsen 1955,

p. 146). (4) In the southwestern United States, four or five of the seven 20-yr periods from the 1840s to the 1980s appear to have been characterized by drought of the magnitude observed between 1941 and 1960 (fig. 1; Lehman 1969; Norwine 1978; Neilson 1986). Thus, since the 1840s, $P(\text{wet})$ has approximated 0.3 to 0.4 in the region. As a result, the scenarios using $P(\text{wet}) = 0.3$ and $P(\text{wet}) = 0.6$ would reasonably bracket cluster growth. (5) Predicted stand age structure and temporal development were comparable to those reported for invasions of *Pinus ponderosa* (Pinaceae; see Madany and West 1983), *Larrea tridentata* (Zygophyllaceae; see Chew and Chew 1965), *Pinus monophylla* and *Juniperus osteosperma* (Cupressaceae; see Blackburn and Tueller 1970), and *J. occidentalis* (Young and Evans 1981). In each of these studies, direct measures of plant age indicated woody-plant encroachment into arid and semiarid grasslands beginning in the late 1800s in western North America. (6) Even if age estimates err by 100%, most clusters would still be less than 200 yr old.

Rates of Cluster Development and Physiognomic Change

Once established in grasslands, *Prosopis* facilitated the ingress and establishment of additional woody species. Details of this autogenic succession have been summarized elsewhere (Archer et al. 1988). This model provides a time scale for the process. Species additions to clusters began within 10–15 yr of *Prosopis* invasion, continued at a rapid rate for 35–45 yr, and then became asymptotic at about 10 species per cluster (fig. 3).

Of the dead *Prosopis* plants encountered in previous field surveys (Archer et al. 1988), over 85% were estimated to be less than 30 yr of age at the time of death (table 3). This percentage was probably an underestimate, because remains of small plants would be less persistent than those of larger plants. Individuals over 30 yr old at the time of death were uncommon, indicating that mortality of larger-sized plants was low. The oldest dead plant found had expired at 60–70 yr of age (table 3). In contrast, 11%–19% of the still-living *Prosopis* population was more than 70 yr old and 7%–11% were more than 100 yr old (fig. 5; Archer et al. 1988). Low rates of mortality among plants over 30 yr of age and the potentially long life span of *Prosopis* on dry uplands (minimum observed maximum age of 172–217 yr) suggest that the age-class distribution in figure 5 is that of a young, recently established population developing from a few scattered pioneers (see, e.g., Blackburn and Tueller 1970; Spring et al. 1974; Young and Evans 1981). As more *Prosopis* plants established over time and persisted to seed-bearing age, they provided additional seed sources (Mack 1985), which would have contributed to accelerated invasion, primarily in years following drought (Herbel et al. 1972; Archer et al. 1988).

Most clusters also appear to have been initiated since the turn of the century, their numbers increasing geometrically (fig. 4). There was no indication of density-dependent restrictions on recruitment or expansion. Over time, the age distribution of clusters should shift to the right as existing clusters enlarge and competition and space limit the recruitment of new clusters. The observed shift to a higher proportion of larger clusters from 1941 to 1983 (Archer et al. 1988) indicates that this has been happening. Alternatively, the age-class structure in

figure 4 could mean that the probability of clusters (and *Prosopis* plants) persisting more than 50 yr is low. However, this would not seem to be a reasonable interpretation since most species in clusters are vigorous sprouters, capable of persisting over an array of pyric, chemical, and mechanical disturbances (Scifres et al. 1985). Although significant mortality was observed among clusters smaller than 5 m² (i.e., less than 35 yr old) during the 1950s drought, larger clusters persisted, and recruitment in the subsequent pluvial period exceeded losses during the drought period (Archer et al. 1988). Thus, succession at this site appears to be proceeding at a geometric rate from one state (grassland) to another (woodland) and has not been a cyclic replacement series such as that described by Yeaton (1978) in a Chihuahuan ecosystem.

As new clusters are initiated and existing clusters expand, coalescence will become increasingly probable. However, edaphic heterogeneity, cluster density, and proximity to other clusters may regulate the rates of cluster expansion. Although it was not possible to partition variation in cluster growth attributable to these parameters, instances of coalescence of clusters were observed from 1960 to 1983 (Archer et al. 1988). Since 95% of the clusters were within 15 m of one another, a radial expansion of 7.5 m would result in coalescence with other similarly expanding clusters under conditions of constant density. Among clusters smaller than 250 m², these radial increases would be realized in 50–70 yr under the $P(\text{wet}) = 0.6$ and the $P(\text{wet}) = 0.3$ precipitation regimes, respectively. For clusters 250–1000 m² in area, this expansion would occur in 120 to 160 yr. If mesquite establishment in herbaceous zones continues, cluster densities will increase, and the time to coalescence may decrease. The rate of appearance of new clusters is determined primarily by factors regulating the ingress and establishment of *Prosopis*.

Why Has 'Prosopis' Invasion Occurred Only Recently?

Although the potential natural vegetation of the Rio Grande Plains has been classified as grassland and savanna (Küchler 1964), the current woody flora has probably been in this area throughout the Holocene (Smeins 1983), perhaps restricted to escarpments, caliche ridges, drainages, and riparian zones. *Prosopis*, for example, was a part of the Pliocene flora in southern California (Axelrod 1937), and wood of *Prosopis* species has been recovered in southern Texas from archaeological sites dated to 3300 yr ago (Hester 1980). Johnston (1963) presented evidence that the geographical range of *Prosopis* has changed little in the past 300–500 yr and suggested that it has merely increased in stature and abundance within its historical range. Numerous historical accounts from the early 1800s described landscapes of southern Texas as open prairies with woody plants confined to water courses (Bogusch 1950). Palmer (1871), Tharp (1926), and others have suggested that the spread of *Prosopis* has been recent and lateral, from wooded drainages to upland prairies. Model results (figs. 4, 5) are in accord with these historical observations and indicate that 100–200 yr ago the upland landscape at this site would have been sparsely dotted with clusters of woody plants. Many landscapes in the region are now dense thorny woodlands. What precipitated this apparently rapid shift in physiognomy over the last century?

Overgrazing, fire suppression, and climatic change have been cited as proximate causes of woody-plant invasion into grasslands (see, e.g., Hastings and Turner 1965), and all have probably interacted in complex ways. The relative importance of these factors in effecting a physiognomic shift may vary, depending on the spatial and temporal scales on which they are examined. On a large scale, climate appears to dictate vegetation physiognomy (Box 1981) and dynamics in arid and semiarid systems (MacMahon 1980; Austin et al. 1981; Chew 1982). In some cases, climate-induced changes have been erroneously ascribed to grazing (Western and van Praet 1973; Branson 1985). In other instances, grasslands established under past climatic regimes may be only marginally supported by the present climate and, as such, are prone to woody-plant encroachment (Neilson 1986). Oscillations between different climatic regimes (Stockton and Meko 1975; Mitchell 1980) may have also effected regional shifts in plant-recruitment patterns to promote episodes of establishment of woody life forms but not necessarily their local extinction (Neilson and Wullstein 1985; Neilson 1987). However, as spatial and temporal frames of observation are diminished and resolution increased, broad-scale climatic patterns cannot account for the existence of small-scale patterns, and biotic processes assume greater importance in regulating community structure (Prentice 1986). In this regard, Rummel (1951) and Madany and West (1983) have demonstrated that savannas protected from livestock grazing have been maintained despite low fire frequencies. In contrast, nearby edaphically similar sites subjected to grazing had substantially higher densities of woody plants that became established after the introduction of livestock. At their sites, savannas have persisted when grazing was prevented, even though the climate may have changed since the 1800s. Thus, climatic changes such as those of the past 100–200 yr may have been necessary, but by themselves were perhaps not sufficient, to have caused a shift from grassland or savanna to woodland.

In arid and semiarid regions where fire is uncommon, the balance between grasses and woody vegetation may be regulated by the ratio of topsoil to subsoil moisture (Walter 1979; B. Walker et al. 1981). Grasses, with their fibrous root systems, would be superior competitors for water in the topsoil, whereas woody plants more effectively access deeper soil moisture with their extensive taproot systems. Where water-holding capacity of the topsoil is relatively high, grasses may significantly influence the distribution of soil water and the growth of woody plants. Field experiments (Soriano and Sala 1983; Knoop and Walker 1985) support this hypothesis and indicate that factors reducing the ratios of topsoil to subsoil moisture could cause savannas to develop into woodlands. Climatic changes contributing to a decrease in the topsoil-subsoil moisture distribution include an increase in annual rainfall, shifts from small, frequent precipitation events to large, infrequent events, and/or a shift toward increased winter precipitation. The latter appears to have occurred in the North American Southwest since the turn of the century (Hastings and Turner 1965; Neilson 1986). On a local scale, extensive grazing could enhance the percolation of water to the subsoil by reducing the transpiring leaf area and decreasing the root initiation and extension, biomass, and resource uptake of grasses (see, e.g., Carmen and Briske 1982; Archer and Tieszen 1983; Caldwell et al. 1987). These adverse effects of defolia-

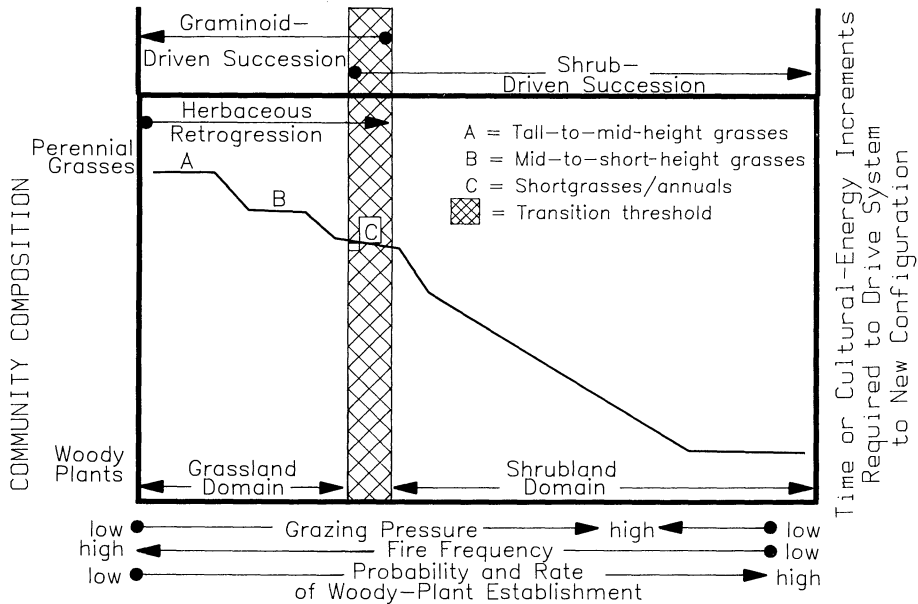


FIG. 6.—Conceptual diagram of threshold changes in community structure as a function of grazing pressure. Within the grassland domain, grazing alters the composition and productivity of herbaceous species while decreasing fire frequency and intensity, thereby increasing the probability of woody-plant establishment. If grazing pressure is reduced before some critical threshold, succession toward higher-condition grasslands may occur. However, if sufficient numbers of woody plants become established, shrub-driven successional processes begin to predominate and the site moves toward a new steady-state configuration. Once in the shrub-land or woodland domain, the site will not revert to grassland after grazing has ceased, especially if the displaced grasses had originally established under a different climatic regime. Anthropogenic manipulation can alter grass-shrub mixtures, but subsequent succession may result in a rapid return to a community dominated by woody plants.

tion would reduce the ability of grasses to limit the moisture recharge of deeper soil layers and competitively exclude invading woody plants. Grazing by ungulates may also increase soil surface strength and decrease soil porosity and organic matter such that the recruitment of woody plants is favored relative to grasses (Braunack and Walker 1985).

The conceptual model in figure 6 illustrates how grazing might cause a shift from grassland or savanna to shrub land or woodland at a site. Grasses are able to sustain some degree of grazing pressure before retrogressing to new assemblages of herbaceous species (e.g., state A). However, as grazing pressure increases, community structure is altered and the composition of herbaceous species shifts (e.g., state B) (Launchbaugh 1955; Humphrey 1958; Smeins et al. 1974; McNaughton 1983; Archer et al. 1987). When grazing pressure is reduced or removed, soil, seed bank, and vegetative regeneration potential remain conducive to the reestablishment of the preceding species assemblages (state A). However, if grazing pressure is maintained (with the natural consequence of reduced fire frequency and intensity) and woody plants begin to establish, a transitional threshold is

eventually reached (B. Walker et al. 1981). At this point, new successional processes begin to drive the system, and autogenic modification of soils and microclimate by invading shrubs facilitates a conversion in physiognomy similar to that described in a previous study (Archer et al. 1988). Over time, a stable shrub-land or woodland system may develop, and the modification of soil, seed bank, and vegetative regeneration potential makes it unlikely that this new assemblage will revert to grassland, even following a curtailment of grazing (see, e.g., Niering and Goodwin 1974; B. Walker et al. 1981; West et al. 1984; Hobbs and Mooney 1986). This would be particularly true if the displaced grasses had originally established under a different climatic regime (Neilson 1986). Once in the shrub-land domain, fire or anthropogenic modification (herbicides, mechanical manipulation) may drive the system back toward a grassland configuration, but the inertia is large and the conversion may be short-lived.

Because of the pivotal role of *Prosopis* in cluster formation and development (Archer et al. 1988), factors regulating its ingress and establishment in grasslands are of primary importance in the Rio Grande Plains. The age structure of clusters (fig. 4) and mesquite plants (fig. 5) represent net survival (Harper 1977). Such data do not indicate the extent to which population structure has been shaped by variation in recruitment versus mortality. As discussed above, *Prosopis* plants and clusters more than 30 yr old appear to be fairly persistent. Thus, the shapes of the age-frequency curves may largely reflect variation in recruitment rates over time.

Two primary components of recruitment are dispersal and establishment. Before the introduction of livestock, dispersal limitations may have kept *Prosopis* densities low on grasslands (Janzen 1986; J. Brown and Archer 1987). Alternatively, although native herbivores may have been disseminating mesquite seeds, few propagules established in grasslands (J. Brown and Archer 1989). Those that did may have been kept low in stature by recurring fire. With the introduction of cattle, sheep, and horses, all effective agents of mesquite seed dispersal (Mooney et al. 1977), *Prosopis* abundance would have subsequently increased. Livestock appear to be an especially effective vector of *Prosopis* seed dispersal: not only do they transport large numbers of seeds away from parent trees harboring host-specific seed and seedling predators, but they deposit the seeds in a viable form capable of germinating in a nutrient-rich medium (dung) in areas where herbaceous interference and the probability of fire have been reduced by grazing (Glendening and Paulsen 1950; J. Brown and Archer 1987). The population age-class structure of *Prosopis* plants and clusters at this site (figs. 4, 5) may thus reflect the synergistic effects of climatic change (Neilson 1986, 1987) and the widespread introduction of livestock since the 1800s (Lehman 1969; Jordan 1981) on alleviating constraints to *Prosopis* dispersal and establishment.

SUMMARY

At savanna woodland sites in southern Texas, discrete clusters of woody plants form in herbaceous clearings following the invasion of mesquite (*Prosopis glandulosa* var. *glandulosa*), an arborescent legume. The growth rate of these clusters

has been shown to vary with precipitation and size. Based on field data and a knowledge of mechanisms of woody-plant successional processes, a simulation model was developed to estimate the rates of growth and development of these woody-plant assemblages on sandy-loam uplands under different precipitation regimes.

In the simulation, the establishment of other woody species beneath invading *Prosopis* occurred within 10–15 yr. As a cluster developed around the *Prosopis* nucleus, species richness increased rapidly for 35–45 yr and became asymptotic at 10 species per cluster. The estimated age of the oldest *Prosopis* plant found in clusters was 172–217 yr. However, model-derived size-age relationships predicted that most (90%) clusters and mesquite plants at the site are less than 100 yr old. A lack of field evidence of mortality among large clusters and *Prosopis* plants suggests that populations are young and expanding geometrically. There was no evidence of density-dependent restrictions on recruitment or expansion. Thus, as new clusters are initiated and existing clusters expand, coalescence to continuous canopy woodlands may eventually occur.

Predicted long-term mean radial trunk growth of *Prosopis* (0.8–1.9 mm/yr) was reasonable in comparison with short-term field measurements on *Prosopis* in other, more-mesic systems (2–4 mm/yr). Model output was also consistent with historical observations suggesting that the conversion of savannas to woodlands in the Rio Grande Plains has been recent and coincident with both heavy grazing by livestock and seasonal shifts in precipitation that began in the late 1800s. This is in agreement with woody-plant invasions documented in other North American arid and semiarid systems by the direct aging of woody plants.

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