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Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A.

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Abstract. The potential natural vegetation of southern Texas and northern Mexico has been classified by plant geographers as savanna. However, many of the present landscapes in this subtropical region are dominated by thorn woodlands. Evidence for replacement of grasslands and savannas by woodlands is based largely on historical accounts, many of which are conflicting. This paper reviews and integrates a series of recent studies addressing

the following questions: (1) Have woodlands replaced grasslands or savannas? (2) If there was a physiognomic conversion (a) what successional processes were involved; (b) what time scale would have been required; and (c) what were the causes?

Key words. *Prosopis glandulosa*, succession, disturbance, grazing.

INTRODUCTION

Savannas are characterized by the dual significance of herbaceous and woody plants. Factors regulating the balance between these contrasting plant lifeforms through time include climate, soils, disturbance (e.g. fire, grazing) and their interaction. Changes in one or more of these factors may enable one lifeform to increase and/or the other to decrease. In many systems, increases in woody plant abundance are accompanied by decreases in herbaceous production and undesirable shifts in composition. Once such shifts in composition and production have been effected, succession to previous states may be slow or may not occur at all. As a result, progressive management strategies that minimize the probability of shifts to increased woody cover should be developed for existing savannas. An understanding of factors regulating the mixture of herbaceous and woody plants in savannas may enable us to identify disturbance and transition thresholds and thereby anticipate undesirable changes in plant community structure and adjust land management practices accordingly. In areas where high levels of woody plant cover already exist, anthropogenic manipulation (fire, herbicides, mechanical treatments, seeding, etc.) may be used to enhance herbaceous productivity. However, effectiveness of such manipulations may depend on their type, timing and sequencing (Scifres *et al.*, 1983), placement on the landscape (Scifres *et al.*, 1988) and subsequent management practices.

Quantitative and historical assessments suggest woody plant dominance has increased substantially in grasslands and savannas during the last 50–300 years in many parts of the world, including Africa (Barnes, 1979; van Vegten, 1983), Australia (Harrington, Wilson & Young, 1984), South America (Schofield & Bucher, 1986; Bucher, 1987),

India (Singh & Joshi, 1979) and North America (Buffington & Herbel, 1965; Blackburn & Tueller, 1970; Herbel, Ares & Wright, 1972; Hobbs & Mooney, 1986). Remaining grasslands and savannas may become increasingly susceptible to woody plant encroachment with the anticipated global climatic changes (Emanuel, Shugart & Stevenson, 1985a, b). Successful management of savannas will require an understanding of their stability and resilience at appropriate spatial and temporal scales. To achieve this understanding, answers to two questions are paramount: (1) What kinds, frequencies or intensities of use might cause long-lasting, undesirable changes in composition and productivity, and (2) How much can a savanna change and still recover its original composition (Walker, 1985)?

A transition from grassland or savanna to shrubland or woodland may result (1) if climate and/or disturbance regimes change to (a) enable native woody species to extend their geographic range or (b) increase in stature and density within historical ranges; or (2) if introduced woody species successfully establish and reproduce. Although encroachment of woody plants into grasslands and increased densities of woody plants in savannas have been widely observed, the rates, patterns and dynamics of the process and its causes have seldom been quantified.

The Rio Grande Plains of southern Texas and northern Mexico offer some distinct examples of processes involved in the physiognomic conversion of grasslands and savannas to woodlands. The potential natural vegetation of this region has been classified as *Prosopis–Acacia–Andropogon–Setaria* savanna (Küchler, 1964). However, much of the present vegetation is subtropical thorn woodland (Blair, 1950). A component of the Tamaulipan Biotic Province (Dice, 1943), the thorny shrubs and small trees in

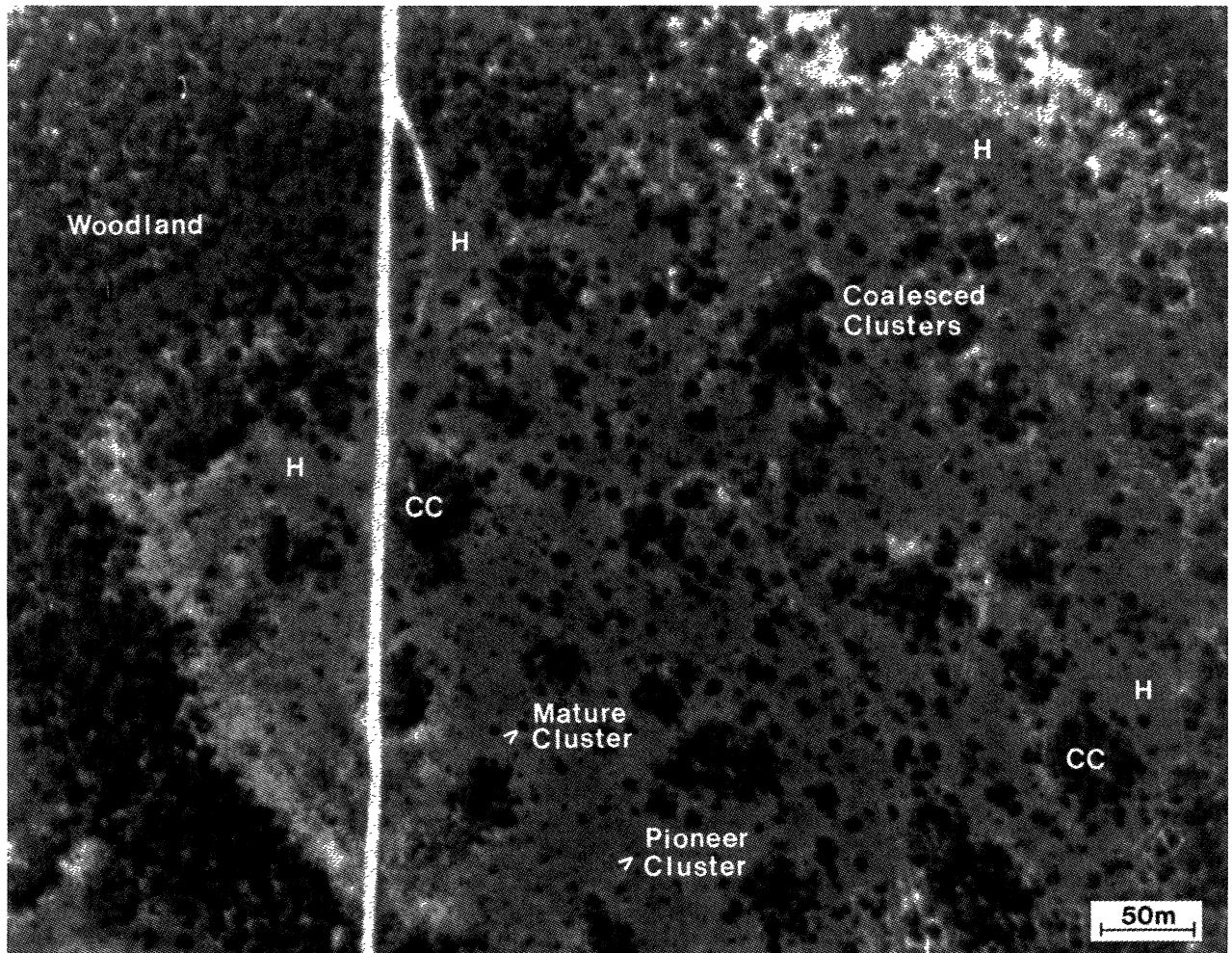


FIG. 1. Aerial view of a two-phase pattern of discrete clusters of woody vegetation embedded in a grass-dominated herbaceous matrix (H) on the La Copita Research Area in southern Texas, U.S.A. The clusters, which were organized about a *Prosopis glandulosa* nucleus (Fig. 2), represented chronosequences (Fig. 3) in which species composition at later stages of development were similar to those of adjacent closed-canopy woodlands (Archer *et al.*, 1988). It is hypothesized the two-phase pattern, which characterized 80% of the research area, is moving toward a closed-canopy woodland as new clusters are initiated with existing clusters expand (Table 2) and coalesce (cc = coalesced clusters) (Fig. 6).

this system have counterparts throughout much of the world's tropical and subtropical zones (Brown, 1982). In many instances it is believed these vegetation types have replaced large areas of former grasslands (cf. Schofield & Bucher, 1986). However, the basis for this contention is largely from indirect, historical sources, many of which are conflicting (Malin, 1953). This paper reviews the results of a recent series of studies in southern Texas which have focused on the following questions: (1) Have thorn woodlands replaced grasslands or savannas in recent history, and (2) If there was a physiognomic conversion (a) what were the mechanisms involved; (b) what were the rates and dynamics of the process; and (c) what were the causes?

STUDY SITE

The research reviewed in this paper was conducted on the Texas Agricultural Experiment Station's La Copita Research Area 65 km west of Corpus Christi, Texas

(27°40'N; 98°12'W). The site has a history of moderate to heavy cattle grazing since the mid-1800s. Topography is generally level with slopes $\leq 3\%$. Elevation ranges from 75 to 90 m. The climate is subtropical with warm winters and hot summers. Mean annual temperature is 22.4°C and the growing season is 289 days. Average annual rainfall is 680 mm with maxima in May and September.

The predominant vegetation of the area was savanna parkland (Fig. 1) consisting of discrete clusters of woody vegetation organized beneath the arborescent legume, honey mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa*). Common understorey shrubs beneath the *Prosopis* canopy were *Zanthoxylum fagara* (L.), a slightly coriaceous (leathery-textured), broad-leaved evergreen; *Celtis pallida* (Torr.) and *Condalia hookeri* (M. C. Johnst.), each malacophyllous (herbaceous) and deciduous; *Diospyros texana* (Scheele.) a coriaceous, broad-leaved evergreen; *Schaefferia cuneifolia* (Gray) and *Ziziphus obtusifolia* (T. & G.), each drought deciduous; and *Berberis trifoliolata* (Moric.),



FIG. 2. A *Prosopis*-mixed shrub cluster at an advanced stage of development (see Fig. 3 for additional details).

a sclerophyllous evergreen (plant nomenclature follows Correll & Johnston, 1979). Vegetation in herbaceous zones was dominated by C₄ grasses such as *Paspalum setaceum* (Michx.), *Bouteloua rigidiseta* (Steud.), *Chloris cucullata* (Bisch.), *Aristida* spp., *Bouteloua trifida* (Thurb.) and *Cenchrus incertus* (M. A. Curtis). Herbaceous dicots included

Evolvulus spp., *Eupatorium* spp., *Verbesina* spp. and *Zexmaniania hispida* (H.B.K.). This savanna parkland vegetation complex occurred on fine sandy loam to sandy clay loam soils and occupied 80% of the 1093 ha research area. See Scifres & Koerth (1987) for more complete descriptions of soils, vegetation and climate.

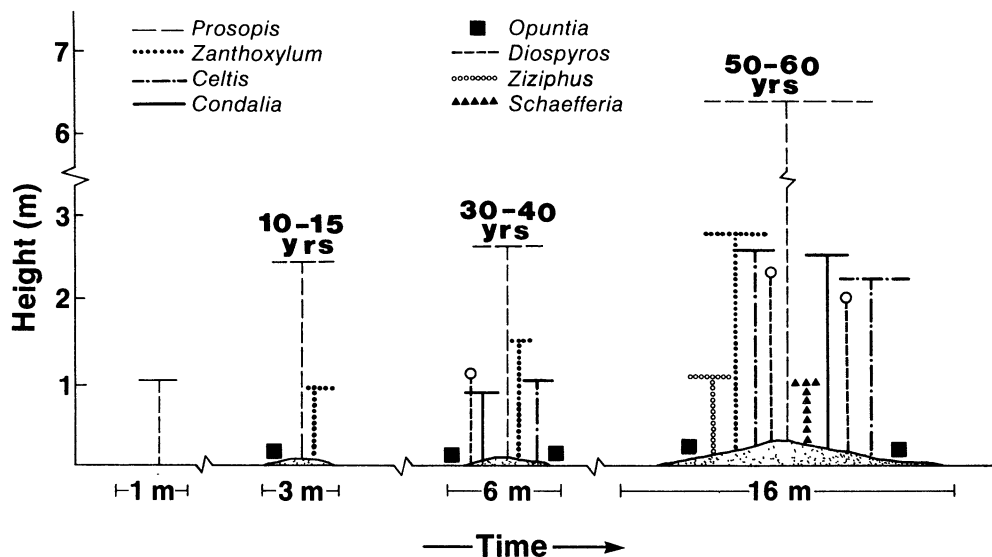


FIG. 3. Development of woody clusters on sandy loam uplands in southern Texas (from Archer *et al.*, 1988). It is hypothesized *Prosopis glandulosa* invades herbaceous zones and (1) adds vertical structure which attracts birds disseminating seeds of other woody plants; and (2) modifies soils and microclimate to facilitate germination and/or establishment of the subordinate woody species. The first woody species appear 10–15 years after *Prosopis* establishment; within 60 years clusters average thirteen woody species (Archer, 1989).

HAVE SAVANNAS BEEN CONVERTED INTO WOODLANDS IN RECENT HISTORY?

Inferences from patterns of succession

Sandy loam uplands on the research site were characterized by distinct clusters of woody vegetation embedded in a matrix of C_4 grasses (Fig. 1). Initial investigations focused on quantifying the structure of woody clusters and examining the herbaceous zone for seedlings and saplings of woody plants. Field data (Archer *et al.*, 1988) indicated: (1) although seedlings and samplings of eight woody species were encountered in the herbaceous matrix the great majority, in terms of density and frequency, were of one species, *Prosopis glandulosa*; (2) individual woody clusters ranged in size from 1 to 16 m diameter; (3) there was typically one *Prosopis* plant centrally located in each cluster and it was usually the largest plant, in terms of height, basal diameter and canopy area (Fig. 2); (4) the number of subordinate woody species in clusters, which ranged from one to fifteen, was positively correlated with the size of the *Prosopis* plant ($r^2 = 0.86$); (5) with the exception of *Prosopis*, most species in clusters would be bird-dispersed; and (6) species composition and relative abundance in large clusters was comparable to that of closed-canopy woodlands in neighbouring ephemeral drainages. These data suggest *Prosopis* colonized grass-dominated sites and served as the nucleus of cluster organization, apparently facilitating the ingress and/or establishment of additional woody species otherwise restricted to other habitats (Fig. 3).

As the abundance of woody species beneath *Prosopis* increased, herbaceous production decreased (Fig. 4). If *Prosopis* plants continue to invade and develop in the herbaceous zones, new clusters will form. At the same time, existing clusters will enlarge as new species are added and canopies of established plants develop. The present savanna parkland may thus represent an intermediate stage in the conversion of a grassland to woodland. Closed-canopy woodlands in the region appear to represent sites where this process has already occurred.

Direct assessments of vegetation change

The above scenario was developed from inferences derived from a space-for-time substitution study of successional patterns. Direct assessments of changes in grass-woody composition of these landscapes using aerial photographs and stable carbon isotopes provide additional evidence that woody plants have displaced grasses.

A comparison of aerial photographs from three different landscapes on the study area indicated total woody plant cover increased on the two-phase upland from 13% in 1941 to 36% in 1983 (Archer *et al.*, 1988). During this same time period, mean cluster area increased from 494 to 717 m² and coalescence of discrete clusters was evident. If this trend continues, the present savanna parkland may develop into a closed-canopy woodland.

Tissues from C_3 and C_4 plants have distinctive $^{13}C/^{12}C$ ratios (Smith & Epstein, 1971) expressed as $\delta^{13}C$. In addition, $\delta^{13}C$ ratios in soil organic matter generally reflect the relative contribution of C_3 and C_4 plants to site productivity

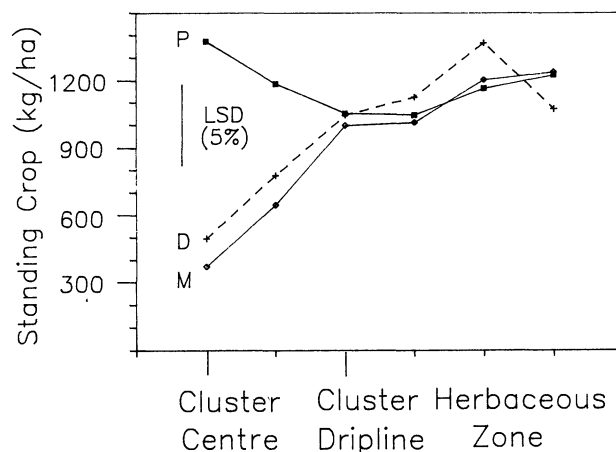


FIG. 4. Herbaceous standing crop (June 1986) along gradients extending from the herbaceous zone into the centre of woody clusters at various stages of development (P = pioneer [e.g. lone *Prosopis*], D = developing, and M = mature [e.g. Fig. 3]). Although herbaceous production was enhanced following *Prosopis* establishment, the subsequent ingress of additional woody species adversely affected this parameter. Bare ground increased from an average of 10% in the herbaceous zone to 45% and 68% within developing and mature clusters, respectively (from Scanlan, 1988).

integrated over long periods of time (Troughton, Stout & Rafter, 1974). The $\delta^{13}C$ values indicate the deviation (‰) of the $^{13}C/^{12}C$ ratio of the sample from that of an international standard. The $\delta^{13}C$ of plants and soils associated with the chronosequence in Fig. 3 were determined as described by Dzurec *et al.* (1985). Woody species in clusters possessed the C_3 photosynthetic pathway ($\delta^{13}C$ range = -27 to -32 ‰), whereas vegetation of grass-dominated zones between clusters was characterized by plants with C_4 pathway ($\delta^{13}C$ range = -13 to -17 ‰) (Table 1). If shrubs have been a long-term constituent of these landscapes, the $\delta^{13}C$ signature of soils beneath them should reflect this and fall in the -27 to -32 ‰ range. However, if C_3 shrubs have displaced C_4 grasses: (1) the soil $\delta^{13}C$ value would be greater (less negative) than -27 to -32 ‰; (2) the degree of departure from the expected ratio would decrease as time of site habitation by shrubs increases; and (3) soil $\delta^{13}C$ values would become less negative with depth along the chronosequence. An analysis of soil organic carbon $\delta^{13}C$ confirmed these predictions.

The organic carbon of soils beneath herbaceous zones was strongly C_4 and reflected the composition of the current vegetation throughout the profile ($\delta^{13}C = -14$ to -18 ‰) (Table 1). In contrast, the mean $\delta^{13}C$ ratio in the upper horizon of soils in the centre of clusters at early and late stages of development was -21 and -23 ‰, respectively. These values were significantly less than the signature of the associated vegetation ($\delta^{13}C$ range = -27 to -32 ‰) and indicate the presence of C_4 -derived carbon on the site. The decrease in $\delta^{13}C$ from -21 to -23 ‰ appears to reflect the additional input of C_3 carbon associated with the passage of time required for *Prosopis* plants and clusters to develop on the respective sites. Strength of the C_4 signature increased to a depth of 60 cm among soils supporting woody vegetation, converging on the values observed for the herbaceous zones.

TABLE 1. Vegetation attributes and $\delta^{13}\text{C}$ values (‰) for vegetation and soil organic carbon along the grassland-to-woodland chronosequence depicted in Fig. 3 (mean \pm SE; $n = 3$) (Archer & Tieszen, unpublished). Pioneer clusters consisted of lone *Prosopis* plants. For $\delta^{13}\text{C}$ values, analysis of variance indicated vegetation state, depth and the vegetation \times depth interaction were significant at $P < 0.05$.

	Herbaceous zones	Pioneer clusters	Well-developed clusters
<i>Prosopis</i> height (m)	—	1.5 \pm 0.1	5.1 \pm 0.6
<i>Prosopis</i> basal diameter (cm)	—	5.7 \pm 1.1	27.0 \pm 2.4
Cluster canopy area (m ²)	—	2.9 \pm 1.2	52.9 \pm 11.8
No. of woody species	0 \pm 0	1.0 \pm 0.0	11.7 \pm 1.5
Vegetation $\delta^{13}\text{C}$			
Shrub layer	—	-27.2 \pm 1.4	-29.6 \pm 0.6
Ground layer*	-13.4 \pm -0.2 ^a	-17.1 \pm 2.8 ^{ab}	-23.0 \pm 1.8 ^b
Soil $\delta^{13}\text{C}$ at depth:			
0–5 cm†	-17.9 \pm 0.4 ^a	-20.7 \pm 0.2 ^b	-23.1 \pm 0.3 ^c
15–30 cm	-14.3 \pm 0.5 ^a	-16.2 \pm 1.2 ^a	-18.3 \pm 0.2 ^b
45–60 cm	-13.9 \pm 0.6 ^a	-14.3 \pm 0.6 ^a	-17.3 \pm 0.3 ^b

* Includes litter.

† Means within a row followed by same letter were not significantly different ($P > 0.05$).

These data constitute direct evidence that shrubs have displaced grasses on the site. But when did these changes occur? To address this question, information on cluster growth rates obtained from a sequence of aerial photographs spanning a 42 year period was used reconstruct site history.

Rates and dynamics of succession

Changes in total woody plant cover and cluster size were quantified for three sites using aerial photographs taken in 1941, 1960 and 1983 and related to patterns of annual precipitation (Archer *et al.*, 1988). Although there was a net increase in woody cover between 1941 and 1983, the development of woody assemblages were markedly affected by variations in annual precipitation. Between 1941 and 1960, a period characterized by a severe 7-year drought, woody cover decreased on each of three sites examined (Fig. 5). The decline in cover was the combined result of a reduction in the density (mortality) of small clusters (area $< 5 \text{ m}^2$), and a reduction in total canopy area and fragmentation of large clusters. In the subsequent pluvial period (1960–83), growth rates of clusters increased (Table 2) along with the density of small clusters (recruitment), more than compensating for reductions in woody cover incurred between 1941 and 1960. Thus, while there were instances of cyclic replacement and/or fluctuation on these sites between 1941 and 1983, there was an overall succession toward woodland. Assuming (1) the processes operational over the 1941–83 period continue; and (2) edaphic or density-dependent factors will not regulate cluster development or distribution, the time to canopy closure may depend on the frequency and sequencing of drought periods (Fig. 6). The validity of these assumptions remains to be demonstrated.

Estimates of cluster growth rates under different precipitation regimes (Table 2) were used to model growth and determine size/age relationships for *Prosopis* plants and the woody clusters that form beneath them (Archer, 1989). This model indicated establishment of woody species be-

neath invading *Prosopis* occurred within 10–15 years (Fig. 3). Species richness increased rapidly from 35–45 years, becoming asymptotic at an average of thirteen species per cluster. Estimated age of the largest *Prosopis* plant found in clusters was 172–217 years. However, 90% of the *Prosopis* plants and clusters on the site appear to be < 100 years of age and the age-class distribution was that of a young population expanding geometrically (Fig. 7). Model projections concur with numerous historical accounts from the late

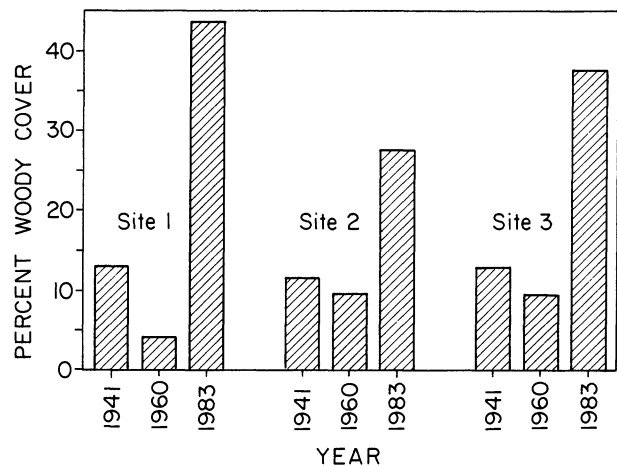


FIG. 5. Changes in total woody plant cover between 1941 and 1983 for three sites on the La Copita Research Area (from Archer *et al.*, 1988). The 1941–1960 period was characterized by a severe 7-year drought in the 1950s, whereas the 1960–83 period received normal to above-normal annual precipitation. Slight decreases in woody cover between 1941 and 1960 were attributed to mortality (disappearance) of small clusters and death of individual plants in large clusters. Increased woody cover between 1960 and 1983 resulted from the initiation of new clusters and rapid growth of existing clusters (Table 2). During the dry 1941–60 period, herbaceous production would have been reduced and dissemination of *Prosopis* seed by livestock was likely substantial. In the subsequent pluvial period, conditions might thus have favoured *Prosopis* recruitment.

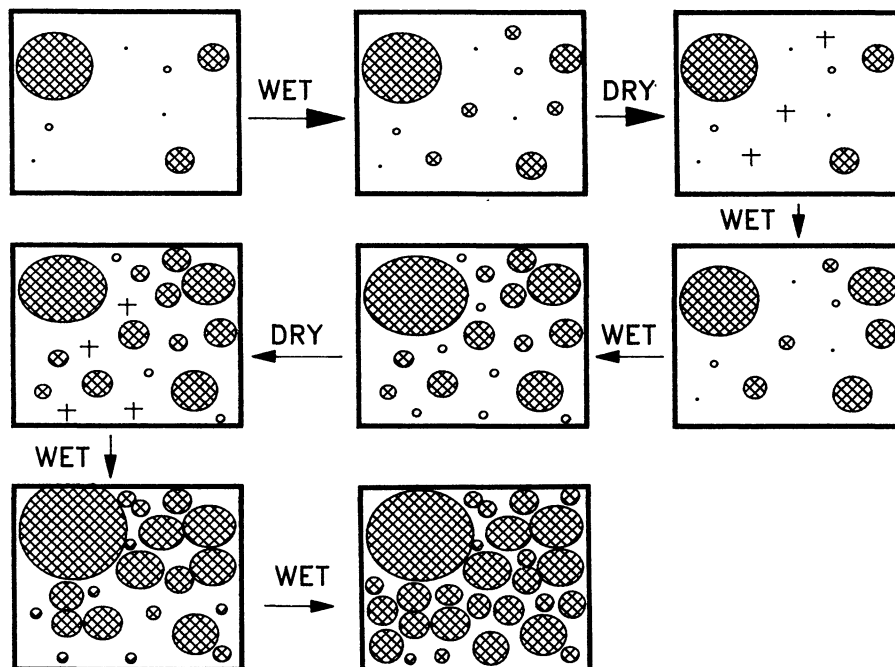


FIG. 6. Hypothesized pattern of succession from savanna to woodland on the La Copita Research Area in southern Texas, U.S.A. Evidence from aerial photographs indicated mortality of small clusters (+) in dry years; however, the appearance of new clusters (●) in normal to above-normal rainfall years more than offset these losses. Although rates of clusters expansion were dynamic, they were generally positive (Table 2). Unless edaphic, pyric or density-dependent processes limit establishment and growth of clusters, the two-phase landscape will develop into a closed-canopy woodland. The rate of transformation may depend upon the frequency and sequencing of dry periods (e.g. Fig. 3).

TABLE 2. Relative growth rates (RGR) of *Prosopis*-mixed shrub clusters in the Rio Grande Plains, Texas, determined by Archer *et al.* (1988) from aerial photographs. 'Dry' denotes growth during the 1941–60 period characterized by a major drought, 'wet' refers to the period of normal to above-normal precipitation from 1960 to 1983. The negative growth among large clusters in the dry period reflects canopy reductions resulting from the loss of individual woody plants.

Cluster size (m ²)	RGR (m ² m ⁻² y ⁻¹)	
	Dry (1941–60)	Wet (1960–83)
<100	0.10	0.16
100–400	0.01	0.03
401–1000	0.01	0.02
>1000	–0.08	0.01

1880s which describe these landscapes as savanna or grasslands with 'mottes' (small patches of woods in a prairie land) (Crosswhite, 1980).

CAUSES FOR SUCCESSION FROM SAVANNA TO WOODLAND

The population structure of *Prosopis* (Fig. 7) and woody clusters on the site indicate something may have happened 100 to 200 YBP to destabilize lifeform interactions and shift the balance to favour woody plants over grasses. Data from aerial photographs indicated *Prosopis* plants and clusters

>30 years old were relatively persistent landscape features (Archer *et al.*, 1988; Archer, 1989). The age class distribution of *Prosopis* in Fig. 7 may therefore reflect enhanced recruitment rather than decreased mortality in recent history. Because of the pivotal role of *Prosopis* in woody cluster formation and development (Fig. 3), factors regulating its ingress and establishment are of primary importance.

Prosopis possesses numerous attributes which make it a successful invader of grasslands: it produces abundant seeds which are potentially long-lived in the soil; germination and establishment can occur across a broad range of soils, water and light regimes; it is capable of fixing nitrogen early in its life cycle; seedlings can vegetatively regenerate following top removal within 2 weeks of germination; survival of 2- and 3-year-old seedlings following very hot fires can exceed 80% and plants can survive prolonged, severe droughts (Archer *et al.*, 1988, and references therein). In addition, root development in *Prosopis* seedlings is rapid (Table 3), enabling them to effectively partition soil moisture with grasses early in their life cycle (Table 4). *Prosopis* is thus an aggressive plant not easily eliminated from a site once established.

Prosopis has been in North America since the Pliocene (Axelrod, 1937) and wood of *Prosopis* dated 3300 YBP has been recovered in archaeological sites in southern Texas (Hester, 1980). Available evidence indicates its geographic range has changed little in the past 300–500 years (Johnston, 1983). These observations, in conjunction with evidence indicating recent increases in abundance on upland sites, suggest *Prosopis* has been present but largely

TABLE 3. Above ground height and biomass, tap root length and biomass and partial root to total plant biomass ratio of *Prosopis* seedlings excavated on 3 May and 22 August 1985 on the La Copita Research Area in southern Texas, U.S.A. Seedlings were newly emerged (cotyledons only = NE; $n = 10$) and recently established with at least one true leaf (EST; $n = 10$) on 3 May and approximately 4 months old (4 mo; $n = 7$) on 22 August. Each value is mean \pm SE. Excavations were terminated at 50 cm (from Brown & Archer, 1990). Nearly 90% of the herbaceous root biomass was within 30 cm of the surface of this site.

Age	Above ground		Below ground		Partial root to total plant ratio (g/g)
	Height (cm)	Biomass (g)	Length (cm)	Biomass (g)	
NE	2.8 \pm 0.2	0.11 \pm 0.01	5.5 \pm 0.0	0.04 \pm 0.00	0.27 \pm 0.09
EST	7.4 \pm 0.8	0.63 \pm 0.11	20.7 \pm 3.7	0.45 \pm 0.12	0.41 \pm 0.13
4 mo	8.1 \pm 1.1	0.68 \pm 0.15	41.3 \pm 5.1	0.73 \pm 0.14	0.52 \pm 0.15

TABLE 4. Best two-factor models, r^2 and significance level ($*P < 0.05$; $**P < 0.01$) for variables regulating stomatal conductance in 1-year-old *Prosopis* seedlings, mature *Prosopis* trees, and *Chloris* tillers. Factors evaluated were % soil moisture (SM) in the upper (<30 cm depth), middle (30–90 cm depth) and lower (>90 cm depth) horizons, vapour pressure deficit (VPD) and soil temperature. No models with more than two factors significantly improved r^2 . All multiple r^2 values were significant at $P < 0.01$. VPD was negatively correlated with conductance; other variables reported were positively correlated (from Brown & Archer, 1990).

Plant category	Variables	Partial r^2	P	Multiple r^2
<i>Chloris</i> tillers	SM-Upper	0.64	**	0.85
	SM-Middle	0.21	**	
<i>Prosopis</i> seedlings	SM-Middle	0.47	*	0.71
	SM-Lower	0.24	*	
Mature <i>Prosopis</i>	SM-Lower	0.65	**	0.80
	VPD	0.15	*	

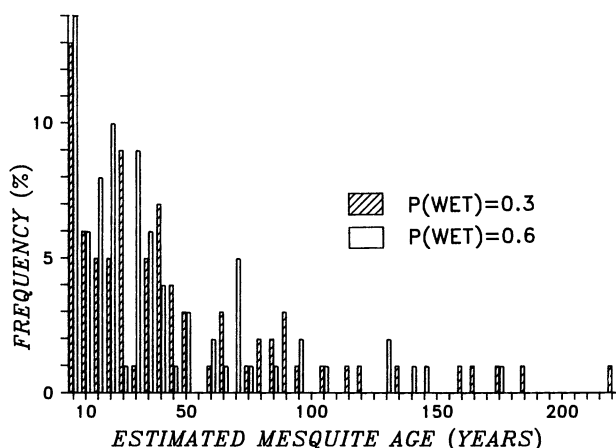


FIG. 7. Age-class distribution of *Prosopis glandulosa* plants on landscapes at the La Copita Research Area, Texas (from Archer, 1989). Projections are based on a size/age model run under two annual precipitation regimes [P(WET) = 0.3 and 0.6] thought to reasonably represent this part of North America since the mid-1800s. P(WET) refers to the frequency with which growth rates in Table 2 were assigned to time-steps in each run of the model. For the P(WET) = 0.3 run, the 1960–83 growth rates (relatively wet period) were randomly assigned to one-third of the time-steps and the 1941–60 growth rates (relatively dry period) were assigned to the other two-thirds of the time-steps. For P(WET) = 0.6, the proportion of time-steps assigned the 1960–83 and 1941–60 growth rates was two-thirds and one-third, respectively.

confined to other habitats (e.g. drainages, playas and escarpments) throughout the Holocene. What has happened in the past 200 years to enable *Prosopis* to increase its abundance in other habitats? Most hypotheses centre around changes in climate, fire and grazing regimes.

There is evidence suggesting climate in recent history may have shifted to favour woody plants over grasses in portions of North America (Neilson, 1986, 1987). However, Madany & West (1983) documented a case in which a savanna was maintained despite low fire frequency (and possible climatic change) on one site, while succession to woodland coincided with the advent of livestock grazing on a nearby edaphically similar site. Data from these respective studies suggest that although climatic change or variation in recent history may have been necessary, it was not sufficient to have caused a shift from savanna to woodland.

The apparent increase in abundance of woody plants since the 1800s on the La Copita site in southern Texas coincides with the development of the livestock (cattle, sheep and horses) industry in that region (Jackson, 1986). Large numbers and high concentrations of cattle, sheep and horses could have facilitated the spread of *Prosopis* by increasing dispersal into new habitats (Table 5) and enhancing seed germination and seedling establishment. *Prosopis* pods are nutritious and may be heavily utilized by livestock, especially during drought periods when the availabil-

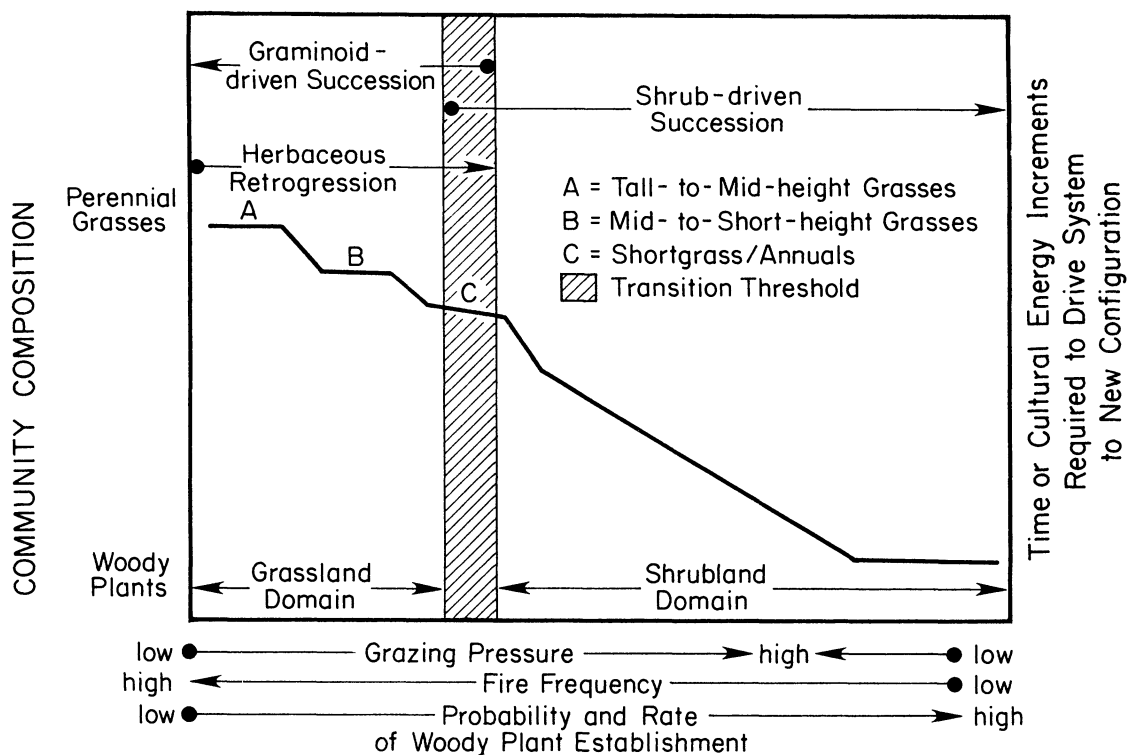


FIG. 8. Conceptual model of changes in community structure as a function of grazing pressure (from Archer, 1989). Within the grassland domain grazing alters herbaceous species composition and productivity, while decreasing fire frequency and intensity. Where seed sources of woody legumes are available, livestock may contribute substantially to dispersal as well as establishment. These factors interact within a variable climate to increase the probability of woody plant establishment. If grazing pressure is reduced prior to some critical threshold, succession toward higher condition grasslands could potentially occur. However, if sufficient numbers of woody plants become established, shrub-driven successional processes begin to move the system toward a new steady-state as a positive feedback situation develops. As woody cover continues to develop (Fig. 6), herbaceous production will decrease (Fig. 4), lowering the carrying capacity for grazers and increasing the grazing pressure in the remaining interstitial zones unless stocking rates are reduced. Once in the shrub- or woodland domain, the soils, seed bank and vegetative regenerative potentials are altered and the site may not revert to grassland or savanna, even following removal of grazing. Anthropogenic manipulation of woody vegetation (e.g. prescribed burning, herbicides, mechanical treatments) can reduce woody cover and enhance herbaceous production. However, without proper grazing management and strategic follow-up treatments, succession back to woodland would be expected.

TABLE 5. Survey results of mean (\pm SE) *Prosopis* seed and seedling density in areas with and without cattle on an upland site in a Texas savanna parkland, August 1985. Canopy refers to seeds and seedlings encountered beneath adult *Prosopis* plants; open refers to occurrences in herbaceous zones (from Brown & Archer, 1987). The absence of seedlings on the area without cattle suggests native wildlife on the site were relatively poor agents of *Prosopis* dispersal.

	With cattle		Without cattle	
	Canopy	Open	Canopy	Open
Area sampled (%)	8	92	9	91
Seedlings m ⁻²	12 \pm 2 ^a	15 \pm 2 ^a	0 \pm 0 ^b	0 \pm 0 ^b
Seeds m ⁻²	33 \pm 7 ^a	11 \pm 2 ^b	33 \pm 8 ^a	0 \pm 0 ^c

* Means within row followed by different letters differed significantly at $P < 0.05$.

ity of grass is low. A high percentage of the hard seeds ingested with the pods escape mastication, are scarified in the digestive tract and deposited in a moist, nutrient-rich medium (dung) away from parent plants harbouring host-specific predators (Brown & Archer, 1987, and references therein). Germination of seed dispersed in this manner can be high and establishment is facilitated because herbaceous interference and fire frequency and intensity have been reduced by defoliation (e.g. Brown & Archer, 1989). In the absence of periodic fire, *Prosopis* plants in uplands would develop in stature, providing (1) seed for additional dispersal; (2) vertical structure attractive to avifauna dispersing seeds of other woody species; and (3) a microhabitat potentially conducive to germination and/or establishment of additional woody species (e.g. altered soils, microclimate and decreased herbaceous biomass; Fig. 4). The punctuated de-

velopment of woody assemblages on these landscapes with a history of heavy grazing by cattle (Fig. 5) may reflect livestock mediation of *Prosopis* seed dispersal, germination, growth and development interacting with the sequencing of dry and wet years.

LANDSCAPE RESISTANCE, RESILIENCE AND MANAGEMENT

Based on inferences from successional processes (Fig. 3), *Prosopis* age-class distributions (Fig. 7) and $\delta^{13}\text{C}$ values of soils associated with woody clusters (Table 1) it appears grasslands or open savannas have become savanna parklands in recent history. If the processes observed between 1941 and 1983 continue, savanna parklands (Fig. 1) may become closed-canopy woodlands (Fig. 6) with extremely low herbaceous productivity (Fig. 4). The conceptual summary in Fig. 8 suggests how and why vegetation may be in the process of shifting from one steady-state toward another.

In the absence of edaphic constraints or climatic change, the continued initiation and expansion of clusters might be arrested by grazing management aimed at (1) reducing dispersal of *Prosopis*; (2) enhancing the capacity of grasses to competitively exclude *Prosopis* seedlings; and (3) enabling periodic use of fire to keep new clusters from forming and existing clusters from increasing in areal extent. Among landscape components where seed bank and vegetative regeneration favour post-disturbance woody plant re-establishment, a long-term sequence of vegetation manipulation technologies may be required to drive the system back toward its previous configuration (cf. Scifres *et al.*, 1983).

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