

Simulated dynamics of succession in a North American subtropical *Prosopis* savanna

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Abstract. A transition matrix model was used to explore the dynamics, rate and potential extent of changes in landscape vegetation patterns on a southern Texas *Prosopis* savanna. Transitions between seven vegetation classes were determined for the periods 1941-1960 and 1960-1983 on aerial photographs of three sites. During these periods, the sites were heavily grazed by cattle and were fire-free. Vegetation states assessed in grids of 20 m × 20 m cells superimposed on photographs ranged from grass-dominated to woody plant-dominated. The 1941-1960 period (denoted DRY) was characterized by prolonged drought, whereas annual rainfall during the 1960-1983 period (denoted WET) was typically normal to above-normal. The 1941 landscape consisted of herbaceous zones (6% of cells), woodland (50% of cells) and savanna parkland (44% of cells with grass/woody plant mixtures). The woodland state was the most stable, with probabilities of no change being 0.970 and 0.873 in WET and DRY periods, respectively. The herbaceous state was least stable, with corresponding values of 0.074 and 0.353.

Past and future landscape structure was modelled by randomly selecting DRY or WET transitions at 20 year time steps. The model was run under a series of rainfall scenarios where the probability of selecting the WET transition matrix (P[WET]) ranged from 0 (DRY always chosen) to 1 (WET always chosen). Historical records indicate P[WET] has approximated 0.3 to 0.4 in the region. The rate of succession to states of greater woody cover increased as P[WET] increased. Forward simulations based on P[WET] > 0.2 suggest the present landscape is unstable and will develop into a closed-canopy woodland within the next 180 years, assuming the processes operating between 1941 and 1983 continue (e.g. grazing by cattle and lack of fire). Reverse simulations concur with historical observations and projections derived from woody plant growth rates in other studies and suggest that 200 to 300 yr BP these landscapes contained a substantially greater proportion of cells dominated by grassland or grassland with scattered woody plants (43 to 74%) than was present in 1983 (19%). Based upon elapsed time between predicted past and future steady states, succession from open savanna to closed-canopy woodland may occur in ca. 400 to 500 yr for P(WET) ≥ 0.33. Arresting or reversing the projected trend may require changes in climate and/or changes in livestock grazing and land management practices.

The approaches employed in this study illustrate how time series maps, aerial photographs and satellite imagery can be analyzed and used to interpret, project and reconstruct local and regional changes in ecosystem structure. Difficulties and limitations associated with the use of Markov chains to model succession are identified and discussed.

Keywords: Aerial photography; Drought; *Prosopis glandulosa*; Simulation; Stability; Transition probability.

Nomenclature: Correll & Johnston (1979).

Introduction

The potential natural vegetation of the Rio Grande Plains of southern Texas has been classified as *Andropogon-Setaria-Prosopis-Acacia* savanna (Küchler 1964; McMahan, Frye & Brown 1984; Diamond, Riskand & Orzell 1987). However, much of the region is presently dominated by a subtropical thorn woodland vegetation complex. Historical accounts suggest this conversion in physiognomy began in the mid- to late 1800s (Johnston 1963; Inglis 1964). Grazing and seed dispersal by domestic livestock, decreased fire frequency and climatic change have been suggested as reasons for such shifts in vegetation structure (Hastings & Turner 1965; Madany & West 1983; Neilson 1986; Brown & Archer 1987; Archer 1989). If grasslands and savannas have been converted to shrublands and woodlands in recent history, a quantification of the rates and dynamics of the process will aid in anticipating and predicting future changes which may occur on other landscapes.

Upland landscapes in portions of southern Texas and northeastern Mexico are characterized by a two-phase pattern of discrete clusters of woody plants dispersed throughout a continuous grassy matrix (Whittaker, Gilbert & Connell 1979) creating a savanna parkland landscape (*sensu* Sarmiento 1984) (Fig. 1). The process

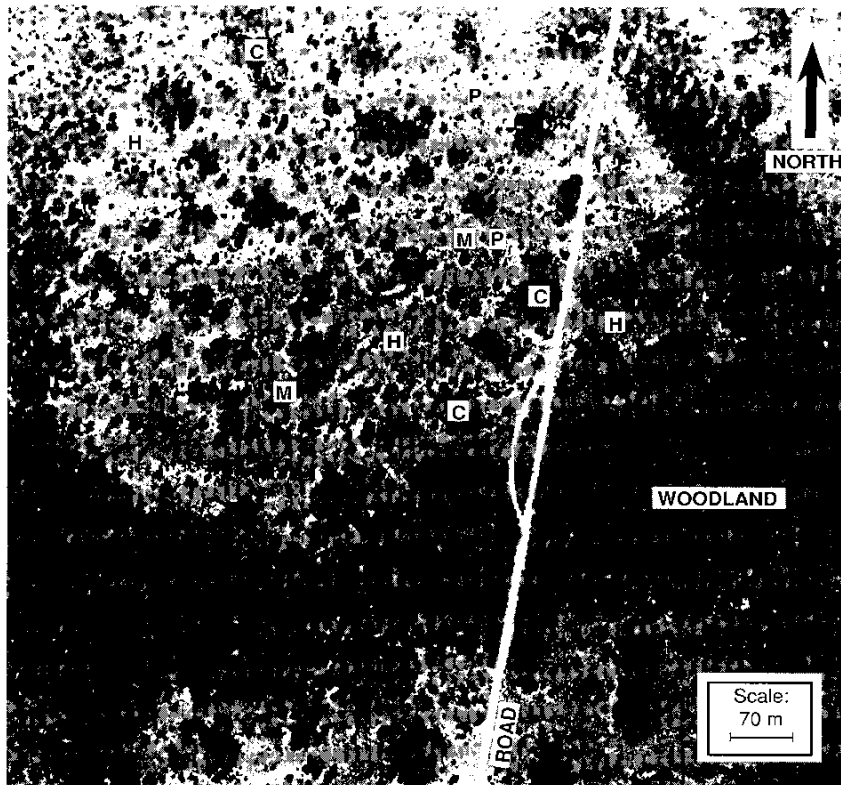


Fig. 1. Aerial photograph illustrating the vegetation states (Table 1) distinguished in a *Prosopis* savanna parkland of southern Texas. A grid of 20 m by 20 m cells was placed on aerial photographs of each of three sites. Transitions between states (Tables 2 and 3) were computed by evaluating grid composition in 1941, 1960 and 1983.

of cluster development begins when mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) establishes in grasslands, modifies soils and microclimate, and facilitates the ingress and establishment of additional woody species (Archer et al. 1988). The result is a landscape comprised of chronosequences of woody vegetation organized around *Prosopis* nuclei. As the abundance of woody plants beneath *Prosopis* increases, herbaceous production decreases (Scanlan 1988). If new clusters are initiated and existing clusters enlarge, coalescence will eventually occur. The present two-phase pattern may thus represent an intermediate stage in the succession from grassland to closed-canopy woodland with extremely low herbaceous productivity. If so, it is of interest to ascertain the rates and dynamics of this process.

A previous analysis of aerial photographs of a savanna site in southern Texas showed the increase in woody plant cover from 16% in 1941 to 36% in 1983 was influenced by annual precipitation (Archer et al. 1988). During a period of drought between 1941 and 1960, mortality among small clusters was 33%. Larger

clusters survived, but often fragmented and decreased in area because of canopy reductions or mortality of individuals comprising the cluster. Few clusters coalesced and total woody plant cover decreased from 13% in 1941 to 8% in 1960. In the decades following the drought, new clusters formed, cluster growth rates increased and substantial coalescence was observed, increasing mean woody plant cover from 8% in 1960 to 36% in 1983. As a result, reductions in woody plant cover during drought periods were more than offset during years with normal or above-normal rainfall.

In this paper, we use probabilities of vegetation transition to explore the dynamics, rate and potential extent of landscape composition changes over longer time-frames. The probabilities of change between various herbaceous and woody vegetation states were determined from aerial photographs bracketing two ca. 20-year periods of contrasting annual rainfall. The resulting transition matrices were then used to project past and future vegetation states under various annual rainfall scenarios. In a larger context, the analytical approaches employed in this study illustrate how time-ordered maps,

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Table 1. Vegetation states distinguished on aerial photographs (Fig. 1) of a two-phase savanna landscape in southern Texas, USA. Descriptions are adapted from Archer et al. (1988). To simplify discussion and interpretation, coalesced cluster and woodland margins (Cm and Wm) have been pooled with C and W, respectively, in most tables and figures.

State	Code	Characteristics
Herbaceous	H	Grasses (<i>Chloris cucullata</i> , <i>Bouteloua rigidiseta</i>) and forbs.
Pioneer cluster	P	Cluster area < 30 m ² . <i>Prosopis</i> plant basal diameter < 10 cm with 4 to 6 woody species in understory.
Mature cluster	M	Cluster area 30 to 300 m ² ; typically 7 to 12 woody species; <i>Prosopis</i> basal diameter 10 to 30 cm.
Coalesced clusters	C	Areas of extensive coalescence; discrete clusters not evident. Up to 15 woody species; numerous <i>Prosopis</i> plants with basal diameters > 40 cm.
	Cm	Coalesced cluster margins. This category was assigned where coalesced clusters (C) did not fully occupy a cell.
Woodland	W	Closed-canopy woodland; typically >15 woody species.
	Wm	Woodland margins; This category accounted for situations where woodlands (W) did not fully occupy a cell.

aerial photographs and satellite imagery can be utilized to interpret, project and reconstruct local and regional changes in ecosystem structure.

Site description

Data were obtained from the Texas Agricultural Experiment Station La Copita Research Area in Jim Wells County near Alice, Texas, USA (27°40'N; 98°12'W) in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. The study sites were savannas comprised of discrete clumps of woody plants organized beneath *Prosopis* (Fig. 1) (Archer et al. 1988). Dominant understory shrubs included *Zanthoxylum fagara*, *Celtis pallida*, *Diospyros texana* and *Condalia hookerii*. Herbaceous vegetation between shrub clumps was dominated by grasses such as *Aristida* spp., *Paspalum setaceum*, *Bouteloua rigidiseta* and *Chloris cucullata*. The sites had been grazed by cattle since the late 1800s.

Climate of the region 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 on the study sites were fine sandy loams derived from sandstones. Elevation ranged from 75 to 90 m (USDA 1979). See Scifres & Koerth (1987) for additional details on soils, vegetation and climate.

Data collection

Probabilities of vegetation transition from one state to another were determined from grids superimposed on enlarged aerial photographs (ca. 1:9000) from each of three sites in 1941, 1960 and 1983. A grid of 20m × 20m cells was superimposed on 1941 photographs of each site and the dominant class of vegetation noted for each cell (Table 1). The same grids were then placed on 1960 and 1983 photographs to coincide with placement on 1941 photographs and states of each cell reassessed. For each vegetation class, the proportion of cells that started in a given class and changed to any other class was calculated. When a cell was occupied by two or more classes of woody vegetation, it was assigned the more advanced class. The numbers of cells evaluated were 550, 332, and 875 on Sites 1, 2 and 3, respectively.

The period from 1941 to 1960 was characterized by several years of severe drought (see Carter 1964), whereas annual precipitation for most years between 1960 and 1983 was normal to above-normal (Fig. 2). For convenience, and because the aerial photos happened to bracket these periods of contrasting annual rainfall, the transition matrices developed for the 1941-1960 and 1960-1983 periods are subsequently referred to as DRY and WET, respectively. The matrices for the two periods were significantly different ($X^2 = 697$; $df = 48$; $p < 0.001$) according to the method of Anderson & Goodman (1957).

Model validation

Transition probabilities determined for Site 1 for each period were used to predict the changes at Sites 2 and 3 over the period 1941 to 1983. As predicted and actual changes were similar for sites not used in the model's development (Fig. 3), the model structure was considered adequate to simulate changes in woody vegetation cover over longer periods. The above procedure was followed using transition probabilities from Site 2 applied to Sites 1 and 3, and using probabilities from Site 3 applied to Sites 1 and 2. The results indicated internal consistency within the data, so all data were pooled to provide the best estimate of transition probabilities (Table 2).

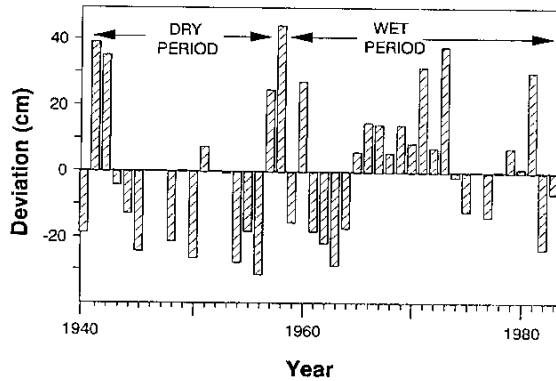


Fig. 2. Deviation of annual rainfall (cm) from the long-term mean (68 cm) for Alice, TX, 15 km from the study site. The DRY period is defined as 1941-1960 and the WET period is 1960-1983.

Model structure

Transition matrix models were developed to simulate changes in frequency distribution of $m = 7$ vegetation classes (Table 1). The inherent problems of transition matrix models are well-known (see van Hulst 1979; Usher 1979), but this approach has provided insight into vegetation dynamics when other approaches are not possible (Enright & Ogden 1979; Lippe, De Smidt & Glenn-Lewin 1985).

Three major assumptions of transition matrix models are (1) stationarity (i.e. the transition probabilities between states are constant over time); (2) the first order Markov property holds [i.e. the transition probabilities depend on the preceding state only and are independent of previous transitions (or history)]; and (3) spatial independence of cells. The assumption of stationarity, seldom valid in most field situations because of stochastic variation in climate and disturbance (Usher 1979; Lippe, De Smidt & Glenn-Lewin 1985), may be overcome by using several transition matrices in the model, with each appropriate for certain environmental conditions (periods of contrasting annual rainfall in our case) (e.g. Burrows et al. 1985). Another approach is to observe the system for a number of time steps and develop a 'mean' transition matrix (Hucenneke & Marks 1987). We used the former method. The Markov property does not hold in situations where past history influences future changes. This would result in spatial heterogeneity in transitions. Although higher order Markov models could be used to account for this, there were insufficient data to address this issue in our models. Our models also treated cells as being spatially independent, when in fact the state of surrounding cells may alter the probability of

Table 2. Probabilities of vegetation change obtained from three sites over consecutive 20 yr periods with contrasting patterns of precipitation (1941-1960 = DRY; 1960-1983 = WET; see Fig. 2). Vegetation states are defined in Table 1.

		WET transitions, 1960-1983						
	W	Wm	C	Cm	M	P	H	
W	0.970 ^a	0.497	0.373	0.132	0.044	0.088	0.019	
Wm	0.027	0.429	0.090	0.126	0.065	0.121	0.086	
C	0.003	0.000	0.328	0.137	0.196	0.036	0.019	
Cm	0.000	0.042	0.119	0.432	0.522	0.170	0.216	
M	0.000	0.000	0.030	0.058	0.109	0.104	0.111	
P	0.000	0.011	0.060	0.095	0.065	0.447	0.475	
H	0.000	0.021	0.000	0.021	0.000	0.036	0.074	

		DRY transitions, 1941-1960						
	W	Wm	C	Cm	M	P	H	
W	0.873 ^a	0.232	0.000	0.012	0.000	0.019	0.000	
Wm	0.075	0.561	0.030	0.040	0.029	0.058	0.029	
C	0.007	0.006	0.515	0.121	0.115	0.019	0.029	
Cm	0.007	0.079	0.242	0.489	0.164	0.112	0.108	
M	0.000	0.006	0.061	0.035	0.212	0.032	0.010	
P	0.035	0.110	0.152	0.224	0.260	0.575	0.471	
H	0.003	0.006	0.000	0.081	0.221	0.184	0.353	

^a = Probability of transition (p_{ij}) from state j (column) to state i (row) in the 20-yr time step from time t to $t+1$.

change between states. For example, an herbaceous cell surrounded by herbaceous vegetation may be less likely to change to a woody state than would an herbaceous cell surrounded by trees and shrubs. This positive feedback may result in complete domination by woody vegetation, a result not possible with our model. A spatially explicit model in which the probability of transition was a function of woody cover in neighboring cells could be used to investigate this possibility.

Our model can be described by a non-stationary Markov chain (Boyer 1979):

$$w_{(t+1)} = P_k \cdot w_{(t)} \tag{1}$$

where $w_{(t)}$ was the $m \times 1$ state vector at time t ; P_k was one of the two $m \times m$ matrices (WET or DRY) of transition probabilities composed of p_{ij} values representing the probability of transition from state j to state i between time t and $t+1$ ($1 \leq i, j \leq m$). The time-step was 20 yr. Although the two periods used to derive the transition matrices were not exactly 20 yr each, we considered it more appropriate to present simulations based on the actual matrices determined at these time-scales, rather than to artificially adjust them to annual transitions. At each time step, a DRY or a WET transition matrix was chosen randomly.

First order, linear, stationary processes (Eq. 1) are ergodic, in that after a large number of time steps a

Table 3. Probabilities of vegetation change backward in time. Transitions were obtained from three sites over consecutive 20 year periods with contrasting patterns of precipitation (1960-1941 = DRY; 1983-1960 = WET; see Fig. 2). Vegetation states are defined in Table 1.

	WET reverse transitions, 1983-1960						
	W	Wm	C	Cm	M	P	H
W	0.776 ^a	0.091	0.026	0.000	0.000	0.000	0.000
Wm	0.114	0.414	0.000	0.035	0.000	0.007	0.114
C	0.030	0.030	0.286	0.035	0.025	0.014	0.000
Cm	0.030	0.121	0.338	0.358	0.138	0.061	0.114
M	0.002	0.015	0.117	0.105	0.063	0.010	0.000
P	0.044	0.258	0.195	0.314	0.550	0.645	0.429
H	0.004	0.071	0.039	0.153	0.225	0.263	0.343

	DRY reverse transitions, 1960-1941						
	W	Wm	C	Cm	M	P	H
W	0.926 ^a	0.285	0.074	0.026	0.000	0.058	0.012
Wm	0.057	0.495	0.015	0.068	0.021	0.042	0.006
C	0.000	0.005	0.250	0.042	0.043	0.012	0.000
Cm	0.003	0.038	0.309	0.445	0.128	0.091	0.087
M	0.000	0.016	0.177	0.089	0.468	0.063	0.143
P	0.014	0.145	0.132	0.272	0.319	0.622	0.528
H	0.000	0.016	0.044	0.058	0.021	0.112	0.224

^a = Probability of transition (P_{ij}) from state j (column) to state i (row) in the 20-yr step from time t to $t+1$.

steady state vector is reached ($w_{(t)} = w_{(t+1)}$), regardless of the initial state vector (Bailey 1964). The lack of stationarity in our model (use of two transition matrices) made it impossible to obtain an analytical solution for the stable state vector, thus simulation was used. Data presented are means for 30 replicate simulations which yielded standard errors of $\leq 2\%$ for the proportion of the landscape cells occupied by each vegetation class. There were no consistent changes observed after 50 time steps in the proportion of the landscape occupied by vegetation classes and these proportions were used as the final (stable) state vector.

To simulate changes backwards in time from 1941, reverse matrices were calculated for each period (Table 3). The reverse matrix for WET transitions was developed using 1983 as the initial conditions and 1960 as the final conditions. The reverse of the DRY transition matrix was calculated using 1960 as the initial condition and 1941 as the final state.

Model experimentation

A series of different precipitation scenarios were simulated such that the probability of using the WET transitions (P[WET]) at each time step ranged from 0.0

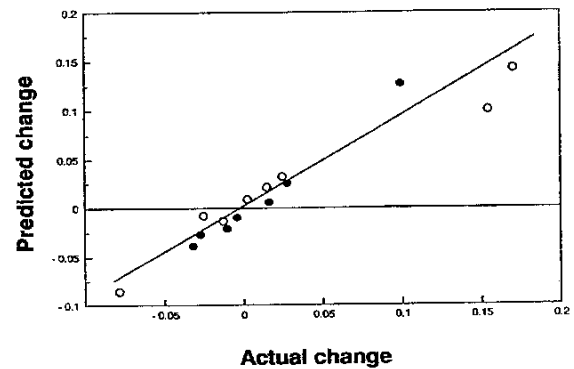


Fig. 3. Predicted versus actual changes in the proportion of area covered by vegetation states (from 1941 to 1983) for two *Prosopis* savanna parkland sites in southern Texas (open circles = Site 2; closed circles = Site 3). Solid line depicts 1:1 relationship between actual and predicted values. The initial state vectors (1941) for Sites 2 and 3 were multiplied by the transition matrices for Site 1 to obtain the predicted changes. Data for all sites were combined (Table 2) on the basis of the good agreement between predicted and actual changes.

(DRY always chosen) to 1.0 (WET always chosen). Reverse simulations were carried out in the same manner as forward simulations. Final state vectors were compared among simulations to determine the impact of precipitation regime.

All our simulations assume that conditions prevailing during the period for which the matrices were calculated will remain for the period being simulated (either future or past). While it is probable that neither past nor future conditions would be exactly the same as those experienced in 1940-1983, this does not invalidate the approach. The simulations are of what may occur or may have occurred, given that management was constant; we do not assume that it was or will remain constant.

A sensitivity analysis was performed to determine which transitions had the most effect on the composition of the stable state vector. This was done by increasing each transition (one at a time) by an amount (δ), while making corresponding adjustments to the value of other transitions from the same vegetation class. For example, when the herbaceous to herbaceous transition was increased by 0.2, the original and modified columns of the transition matrix in Table 2 would be as follows:

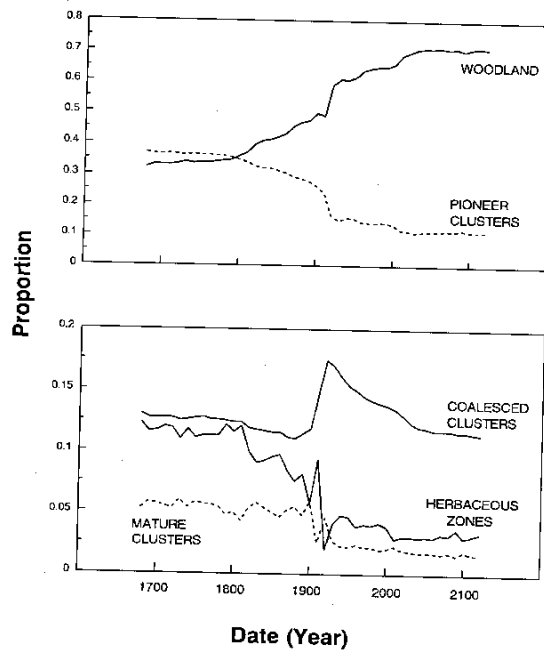


Fig. 4. Mean predicted changes in the proportion of vegetation states (Table 1) in a *Prosopis* savanna parkland in southern Texas based on P[WET] = 0.4. Data represent the mean of 30 simulations backward and forward. Actual data for 1941, 1960 and 1983 were used. Simulation using P[WET] = 0.33 and 0.50 produced similar trends.

Table 4. Initial landscape status and predicted final state vectors (% after 50 time steps) for forward and reverse simulations under a series of rainfall regimes. State vectors represent the percentage of cells on the landscape dominated by each vegetation class.

Vegetation state	Initial conditions	P[WET] ^a						
		0.00	0.20	0.33	0.40	0.50	0.67	1.00
FORWARD								
Woodland	59 ^b	37	57	69	72	77	86	98
Coalesced clusters	17	21	16	13	12	10	06	01
Mature clusters	05	03	02	02	01	01	01	00
Pioneer clusters	17	29	19	13	12	10	05	01
Herbaceous	02	11	06	03	03	03	01	00
Time to stable state (y) ^c		260	<60 ^e	180	180	160	160	140
REVERSE								
Woodland	50 ^d	63	45	37	33	26	19	10
Coalesced clusters	12	08	11	12	13	14	14	14
Mature clusters	06	05	06	07	06	05	05	02
Pioneer clusters	27	20	30	34	38	41	45	50
Herbaceous	06	04	08	09	12	15	17	24
Time to stable state (y) ^e		160	<60	200	200	240	340	320

^a = During simulations, the probability of selecting the WET transition was set to generate different rainfall regimes;
^b = Initial condition was the 1983 state vector;
^c = Time to reach ± 10% of the final woodland percentage;
^d = Initial condition was the 1941 state vector;
^e = The final state vector was similar to initial conditions and time to reach the final state was much shorter than all other cases.

Vegetation state	Original	Modified	
W	0.019	0.000	} Total decrease of 0.2
Wm	0.086	0.000	
C	0.019	0.000	
Cm	0.216	0.139	
M	0.111	0.111	(No change)
P	0.475	0.475	"
H	0.075	0.275	(Increased by 0.2)

Thus, the most extreme change (H → W) was reduced first (to zero in this case). The next most extreme change (H → Wm) was then reduced. This process continued until a reduction totalling 0.2 was achieved. The H → H transition probability was then increased by 0.2. Modifications were made to both matrices at the same time. The W → W transition could not be increased by 0.2, as this would have resulted in a probability ≥ 1. Values greater than 1 are not possible, since a value of one produces an absorbing state (i.e. the final state vector would consist of all elements being in the absorbing state). Thus, no sensitivity to an increase of the W → W transition could be simulated. When the

transition to be increased was a transition to a class of decreased woody cover, the transitions to higher woody cover classes were decreased to compensate for the change. Similarly, when the change was to a class of higher woody cover, the transitions to lower classes of woody composition were correspondingly reduced. This was done for P[WET] = 0.33, 0.40 and 0.50 and for deltas ranging from 0.05 to 0.40 by increments of 0.05, a total of 147 simulations for each delta. Data are presented only for delta = 0.2; all other deltas exhibited similar trends.

The comparative effect on the final state vector of modifying the matrices was determined by calculating the Euclidean distance between vectors from simulations using modified and unmodified matrices. The larger the value, the greater the difference between the two vectors.

Simulation results

To simplify discussion and interpretation, woodland margins (Wm) were pooled with woodland (W), and coalesced cluster margins (Cm) were combined with

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Table 5. Euclidean distance between final state vectors simulated using original (non-manipulated) transition matrices (Table 2) and those generated using modified matrices (see text for description of modification).

(a) P[WET] = 0.33					
	W	C	M	P	H
W	na ^a	0.0316 ^b	0.0069	0.1153	0.0217
C	0.3731	0.0488	0.0212	0.0485	0.0191
M	0.3911	0.0532	0.0365	0.0392	0.0237
P	0.4034	0.0540	0.0360	0.2511	0.0427
H	0.4026	0.0558	0.0369	0.1974	0.0521

(b) P[WET] = 0.50					
	W	C	M	P	H
W	na	0.0107	0.0142	0.0550	0.0075
C	0.4202	0.0512	0.0261	0.0284	0.0240
M	0.4537	0.0559	0.0394	0.0319	0.0286
P	0.4682	0.0564	0.0390	0.1769	0.0398
H	0.4680	0.0574	0.0392	0.1433	0.0439

^a = Not able to be calculated;

^b = This value represents the distance between the state vector obtained using unmodified matrices and the state vector obtained using matrices in which the Coalesced cluster to Woodland transition probability was increased by 0.2, with corresponding reductions in C → M, C → P and C → H. See text for further description of methodology.

coalesced clusters (C). Our forward simulations predicted that the proportion of this landscape inhabited by woodlands will continue to increase at P[WET] > 0.20 (Table 4, Fig. 4). The development of woodlands would occur at the expense of other vegetation classes, with only pioneer and coalesced cluster classes making sizable (ca. 10%) contributions (Table 4 for P[WET] ≤ 0.5). The predicted new steady-states were achieved within 180 yr (9 time steps). At P[WET] = 0.20, the predicted landscape vegetation composition was very similar to the present-day situation.

Reverse simulations were employed in an attempt to reconstruct vegetation history. In the reverse simulations, we assumed a withdrawal of the main effects driving the forward transitions. Thus, if grazing and lack of fire were the main factors driving the forward changes, the reverse simulation would 'undo' these. When the reverse simulations were used to determine a previous 'stable' state vector, and when this vector was then used as the initial state vector for forward simulation, the final 'stable' vector was similar to that produced when using 1983 as the initial vector for a forward simulation. However, these changes occurred more rapidly than those shown in Fig. 4.

Running the model using the reverse transitions in Table 3 enabled us to project what the previous stable composition of the landscape might have been and when

Table 6. Final state vectors obtained from simulations with and without manipulation of transition matrices for P[WET] = 0.33 (other rainfall scenarios produced similar trends). See Table 5 for details on matrix manipulation.

Vegetation class	Transition manipulated			
	Unmodified	Woodland to: Coalesced	Pioneer	Herbaceous
Woodland	0.64	0.34	0.33	0.32
Coalesced clusters	0.13	0.32	0.23	0.23
Mature clusters	0.02	0.04	0.04	0.04
Pioneer clusters	0.16	0.23	0.32	0.27
Herbaceous	0.05	0.07	0.09	0.14

Vegetation class	Pioneer to: Woodland			
	Unmodified	Woodland	Pioneer	Herbaceous
Woodland	0.64	0.78	0.46	0.50
Coalesced clusters	0.13	0.09	0.14	0.12
Mature clusters	0.02	0.01	0.03	0.03
Pioneer clusters	0.16	0.10	0.30	0.22
Herbaceous	0.05	0.01	0.08	0.12

the successional process described by Archer et al. (1988) began. Reverse simulations for P[WET] ≥ 0.33 indicated that 200 to 340 yr BP, 43 to 74% of the landscape cells were dominated by herbaceous vegetation and pioneer clusters, compared to 19% in 1983 (Table 4). We estimated woodlands comprised < 37% of the landscape units ca. 200 to 340 yr BP, versus 59% in 1983. Mature and coalesced clusters were also present in earlier times, but comprised < 20% of the landscape. Based upon the elapsed time between predicted past and future steady states, our model suggests the overall time for succession from open savanna to closed-canopy woodland on these sites would be approximately 400 yr for P[WET] ≥ 0.33 (Table 4). However, the model suggests that the major changes occurred over a much shorter time period beginning in the early to mid-1800s (Fig. 4 shows the situation for P[WET] = 0.4; other probabilities between 0.33 and 0.5 showed similar trends).

Sensitivity analysis indicated that the predicted composition of vegetation classes was most influenced by transitions from woodland to earlier stages, and by pioneer to herbaceous transitions (as seen by the larger euclidean distances in Table 5). This occurred for P[WET] ranging from 0.33 to 0.5. For the same value of delta, the degree of change was generally greater when woodland transitions were altered than when pioneer cluster transitions were altered.

Actual changes resulting from alteration of transition probabilities are summarized in Table 6 for selected cases. Increasing the probability of transition from woodland to any other vegetation class by 0.2 decreased the

predicted woodland cover from 64% to < 34% and increased the predicted combined coverage of pioneer clusters and herbaceous classes from 21% to 41%. Changing the pioneer cluster transitions produced varying results. When the transition to woodland was increased by 0.2, the proportion of landscape cells occupied by woodland increased from 0.64 to 0.78. When the transition to the herbaceous class was increased, the combined proportion of landscape cells occupied by pioneer clusters and herbaceous vegetation increased from 0.21 to 0.34. Increasing the proportion of pioneer clusters that remained in that class rather than moving into mature or coalesced clusters produced a final state composition comparable to that obtained by increasing the pioneer to herbaceous transition.

Discussion

Of the seven 20-yr periods between 1840 and 1980, four to five qualitatively appear to have been characterized by droughts similar to that observed between 1941 and 1960 (Fig. 2) (Lehman 1969; Norwine 1978; Neilson 1986). Thus, since the 1840s, P[WET] has approximated 0.3 to 0.4 in the region. Simulations based on P[WET] > 0.2 suggest the present *Prosopis*-savanna landscape is unstable and is moving towards a closed-canopy woodland, assuming the processes operating between 1941 and 1983 continue (e.g. lack of fire and heavy grazing by cattle). While the interpretation of the forward simulations are ecologically sensible under conditions of grazing and no fire, the reverse simulations are an attempt to reconstruct vegetation history. The reverse simulations suggest the previous stable state of vegetation on these landscapes 200 to 340 yr BP may have been an open savanna (43 to 74% of the landscape composed of herbaceous and pioneer cluster vegetation classes). Our simulations support the hypothesis that vegetation of the present landscape represents an intermediate stage in the conversion of a grassland or open savanna to woodland (Archer et al. 1988). Considering both the forward and reverse simulations, the overall transformation would require ca. 400 yr for $0.33 < P[WET] < 0.67$, although the most striking changes occur over a much shorter time span (Fig. 4). Causes for destabilization of lifeform interactions to favor woody plants over grasses, which were manifest about 150 yr BP, may have included factors associated with interacting and self-reinforcing changes in climatic, fire and livestock grazing regimes [see Archer (1989, 1990); Schlesinger et al. (1990) for discussion and evaluation].

Our transition matrix model reconstructions (Fig. 4, Table 4) are consistent with: (1) historical observations indicating that prior to the 1800s these landscapes were

open savannas with closed-canopy woodlands concentrated in drainages and escarpments (Johnston 1963), or savannas with 'mottes' (i.e. small patches of woods within a prairie land) (Crosswhite 1980); (2) projections of cluster ages derived from growth rates, which indicate most clusters on these landscapes are < 100 yr of age (Archer 1989); (3) direct assessments of vegetation change based on $\delta^{13}\text{C}$ values of soil organic carbon which indicate C3 shrubs have displaced C4 grasses over most of the landscape (Tieszen & Archer 1990); and (4) the timing of woody plant encroachment documented in other arid and semi-arid systems of North America (*Pinus ponderosa*, Madany & West 1983; *Larrea tridentata*, Chew & Chew 1965; *P. monophylla* and *Juniperus osteosperma*, Blackburn & Tueller 1970; and *J. occidentalis*, Evans & Young 1981). Similar rates of savanna-to-thorn scrub conversion also appear to have occurred in the Chaco of Argentina (Schofield & Bucher 1986).

Reversal of the trend toward closed-canopy woodland would require either an increased probability of moving out of the woodland state or an increased probability of pioneer clusters remaining as pioneer clusters or dying (Tables 5 and 6). The fate of pioneer clusters also appears to have a greater impact on long-term trends in woody cover than does the rate of establishment of *Prosopis* plants which initiate pioneer clusters. This inference is substantiated in the herbaceous-to-pioneer cluster transition probabilities (Table 2), where the probability of pioneer clusters appearing in herbaceous zones was comparable for WET and DRY periods (0.475 and 0.471). In contrast, transitions from pioneer clusters to herbaceous vegetation, an indication of cluster mortality, were higher in DRY (0.184) than WET (0.036) periods. This suggests that changes in the abundance of pioneer clusters primarily reflect variation in mortality rather than variation in recruitment. The sensitivity analysis also indicated that herbaceous-to-pioneer transition did not influence the final state vector to the same degree that the pioneer-to-pioneer or pioneer-to-herbaceous transitions did. Thus, while early stages of succession from savanna to woodland may have been regulated by dispersal of *Prosopis* seeds by livestock (Brown & Archer 1987) and their subsequent establishment (Brown & Archer 1989), these factors may have become less important on recent (post-1940s) landscapes where seed producing *Prosopis* plants are relatively abundant and where herbaceous vegetation has experienced retrogressive succession (Archer & Smeins 1990) resulting from long-term heavy grazing.

Stems of *Prosopis* plants are potentially long-lived on this site [maximum ages > 175 yr (Archer 1989)] and *Prosopis* and associated woody species sprout vigorously following damage to stems and trunks. As a result,

the woody component of the landscape vegetation has the capability to persist vegetatively for long periods and regenerate rapidly following severe drought (Carter 1964), frost (Lonard & Judd 1985) and fire (Box, Powell & Drawe 1967). Browsing pressure on the woody plants in this system is minimal and *Prosopis* plants appear capable of establishing from seed in most years (Brown & Archer 1990). A return to the more open savanna or grassland that appears to have characterized this site prior to the 1800s is therefore unlikely, even if livestock grazing were to be curtailed. Although land management practices that utilize prescribed burning, in conjunction with regulated livestock grazing, have the potential to alter the grass/shrub balance to favor transitions to herbaceous vegetation, a long-term, carefully sequenced series of periodic treatments would be required (e.g. Box & White 1969; Scifres et al. 1983).

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