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MARKOVIAN DYNAMICS OF SIMPLE AND COMPLEX
DESERT PLANT COMMUNITIES

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Desert vegetation is commonly dominated by plants with longevities of decades, centuries, and even millennia (Vasek 1980; Steenbergh and Lowe 1983; Goldberg and Turner 1986). Because of the resulting slow rates of population turnover, quantitative representations of the dynamics of desert plant communities are generally lacking. The dynamics of a plant community consist of the flux of individuals through the landscape over time. Patterns of recruitment and mortality responsible for this flux are far better understood for terrestrial plant communities of mesic regions than for those of arid regions. For example, a long history of the study of succession in temperate forests has culminated in general models of vegetational change in terms of species-by-species replacement patterns (Leak 1970; Botkin et al. 1972; Horn 1975; Shugart and West 1980; Huston and Smith 1987). The commonly perceived absence of succession in desert plant communities has led some investigators to suggest that models developed for mesic systems are inapplicable to desert systems (Shreve 1925, 1951; Zedler 1981).

The initial descriptions of the dynamics of a system are instrumental in leading to the discovery and study of underlying mechanisms. The first descriptions of a heliocentric solar system, atomic structure, continental drift, and plant succession in forests were model representations of the dynamics of various systems, all initially formulated without knowledge of the mechanisms responsible. In each of these cases, the accurate descriptions of the movements of objects (planets, subatomic particles, continents, or tree species) through space and time were necessary preliminaries to understanding the natural forces that underlie such movements. Yet, instead of initially studying dynamics per se, much research on desert plant communities has focused on the static structure of these systems (e.g., patterns of distribution, abundance, spatial dispersion, and diversity) and the mechanisms, especially competition, presumed responsible for this structure (Beals 1968; Woodell et al. 1969; King and Woodell 1973; Yeaton and Cody 1976;

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Yeaton et al. 1977; Fonteyn and Mahall 1981; Phillips and MacMahon 1981). Rather than continuing in this vein, I first attempt to unravel and describe the dynamics of desert plant communities by studying spatial and temporal patterns of recruitment and mortality. Only after these dynamics are deduced do I consider possible underlying mechanisms.

STUDY AREAS

I studied structurally simple shrub communities near Dateland (Yuma Co.), Arizona (32.8°N, 113.6°W; elevation 128 m) and San Luis (Yuma Co.), Arizona (32.5°N, 114.6°W; elevation 92 m) between April 1985 and September 1986. These sites are located in the Lower Colorado River Valley vegetational subdivision, the largest and most arid portion of the Sonoran Desert (Shreve 1951; Turner and Brown 1982). Average annual precipitation at Dateland and San Luis is approximately 112 mm and 55 mm, respectively. The topography of the sites is nearly flat with deep and sandy, aeolian-derived soils. The vegetation consists primarily of the codominant shrub species *Larrea tridentata* and *Ambrosia dumosa*, which form the most widespread vegetation type in both the Sonoran and Mojave deserts (Shreve 1942; Turner and Brown 1982). The perennial bunchgrass *Hilaria rigida* is a minor component of the vegetation at each site.

I studied more-diverse Sonoran Desert plant communities within the Arizona Upland vegetational subdivision (Shreve 1951; Turner and Brown 1982) at Saguaro National Monument, Tucson Mountain Unit (Pima Co.) (32.3°N, 111.2°W; elevation 700–800 m), where the average annual precipitation is 280 mm. The study areas were located along a bajada gradient parallel to Mile-Wide Road bordering the southern boundary of the park. Three bajada sites (upper, middle, lower) with slopes from 1° to 2° were studied between March and September 1985.

Additional observations on species-rich assemblages were conducted in March 1984 at Punta Chueca, 40 km north of Bahía Kino, Sonora, Mexico (29.0°N, 112.2°W; elevation 30 m). This bajada site is located in the Central Gulf Coast vegetational subdivision of the Sonoran Desert (Shreve 1951; Turner and Brown 1982) and receives an annual average of 180 mm of precipitation.

METHODS

Within 8-ha study areas at the Dateland and San Luis sites, cover and density data were measured in 40 100-m² circular plots centered on randomly chosen coordinates. Average canopy width, height, and basal diameter were measured for all *Larrea* and a randomly chosen subsample of *Ambrosia* occurring within the plots. Total numbers of live as well as dead individuals of each species were recorded from each plot. Canopy widths were used to calculate areas covered by individual shrubs. For each species, density times the mean canopy cover per individual was used to estimate the total canopy cover per species.

Larrea and *Ambrosia* shrubs with basal trunk diameters of at least 5 mm but less than 40 mm and 15 mm, respectively, were arbitrarily designated as young individuals. Individuals within these size categories do not yet exhibit the stem-

axis splitting that gives rise to multiple basal stems. Growth rings were counted in polished cross sections prepared from the trunks of a sample of young individuals. To determine whether these were annual growth rings, the cambiums of several young *Larrea* shrubs were scarred on October 4, 1985, at the Dateland site. Removal of a 1-mm-wide strip of outer bark and cambium from the base of the trunk resulted in subsequent secondary xylem deposition around the entire perimeter of the trunk except where the cambium was removed. Even after healing, the scar provided a permanent marker that distinguished the wood deposited before and after the cambium was removed. Entire cross sections were taken from these individuals approximately 6 mo (April 11, 1986) and 12 mo (September 27, 1986) after the initial date of cambium scarring. The number of growth rings and the amount of secondary xylem deposition since the date of cambium scarring were determined.

In surveys of young plants, a positive association with other plants was scored if the young plant was rooted within the outer perimeter of the canopy of another plant. For these canopy plants, the species, condition (live or dead), average canopy width, and basal diameter were recorded. Distances from each young *Larrea* or *Ambrosia* shrub to the nearest neighboring *Larrea* and *Ambrosia* were measured. Distances were also measured between 40 randomly positioned points and the nearest neighboring live or dead *Ambrosia* and *Larrea*.

For species-rich assemblages, canopy coverage of perennial species was estimated by the point-intercept method. Sample points were spaced at 1-m intervals along randomly positioned, parallel lines. Each survey consisted of a minimum of 10 lines and 300 points. Individuals of different species were designated as young on the basis of size (see table 7). Dimensions such as basal trunk diameter of trees and shrubs or height of columnar cacti were considered the best indicators of relative age because radial trunk growth or apical growth is preserved in secondary xylem deposition and increases in height. Associations between young individuals and other plants were scored in the same manner as at the Dateland and San Luis sites. Species, canopy width, condition (live or dead), and basal diameters of associated plants were recorded.

RESULTS: TWO-SPECIES SYSTEMS

Patterns of Recruitment and Population Turnover

The vegetation at the Dateland and San Luis sites is characterized by its openness. Total canopy cover of perennial plants is only 12.3% at Dateland and 5.4% at San Luis. *Larrea* and *Ambrosia* account for almost all of the canopy cover (table 1).

Young individuals of these two species differ markedly in their microdistributions. Most recruitment of *Larrea* occurs beneath *Ambrosia* canopies. At Dateland, 85.5% of all young *Larrea* plants are rooted beneath canopies of live *Ambrosia* or are positioned next to or within the dense collections of basal stems of dead *Ambrosia* (table 1). Young *Larrea* shrubs are rarely located in areas devoid of perennial plant cover and are completely absent from areas beneath

TABLE 1
DISTRIBUTION OF YOUNG *LARREA TRIDENTATA* AND *AMBROSIA DUMOSA*
WITH RESPECT TO AVAILABLE PLANT COVER

STUDY AREA	TYPE OF PERENNIAL PLANT COVER	PROPORTION OF COVER	RELATIVE FREQUENCIES OF YOUNG INDIVIDUALS IN EACH COVER TYPE	
			<i>Larrea tridentata</i>	<i>Ambrosia dumosa</i>
Dateland	None; perennial plant cover absent	.877	.102	.830
	<i>L. tridentata</i>	.057	0	.060
	<i>A. dumosa</i>	.059	.453	.010
	Dead <i>A. dumosa</i>	*	.402	.100
	<i>Hilaria rigida</i>	.007	.043	0
	<i>n</i>		117	100
San Luis	None; perennial plant cover absent	.947	.327	.919
	<i>L. tridentata</i>	.028	0	.016
	<i>A. dumosa</i>	.025	.204	0
	Dead <i>A. dumosa</i>	*	.469	.065
	<i>Hilaria rigida</i>	.001	0	0
	<i>n</i>		49	62

* Cover values were estimated for canopies of live plants only.

canopies of larger, older *Larrea*. The close spatial association of young *Larrea* with *Ambrosia* is demonstrated by comparing the observed distances between young *Larrea* and the nearest live or dead *Ambrosia* with the distribution of distances between randomly positioned sample points and the nearest *Ambrosia*. The mean distance from the basal stem of a young *Larrea* to the center of the nearest living or dead *Ambrosia* is 26 cm (SD = 21 cm). This mean distance is included within the average radius of a living *Ambrosia* canopy. The mean distance between 40 randomly positioned sample points (representing a hypothetical sample of randomly positioned young *Larrea* plants) and the nearest neighboring *Ambrosia* is 93 cm (SD = 48 cm), which is significantly greater than the observed mean distance between young *Larrea* and *Ambrosia* ($t = 10.38$, $P < 0.001$).

The pattern of *Larrea* recruitment is similar at San Luis. Living *Ambrosia* canopies account for only 2.5% of the cover; yet 20.4% of all young *Larrea* are positioned beneath these canopies. An even greater proportion of young *Larrea* (46.9%) are rooted next to dead *Ambrosia* (table 1). The mean distance between 48 young *Larrea* shrubs and the nearest *Ambrosia* (64 cm, SD = 79 cm) is likewise significantly less than the mean distance between random points and the nearest *Ambrosia* ($\bar{X} = 133$ cm, SD = 60.98 cm; $t = 4.3$, $P < 0.001$).

At both sites, young *Larrea* plants are associated with the larger, presumably older individuals of *Ambrosia* (fig. 1). Although young *Larrea* individuals are commonly associated with remains of dead *Ambrosia*, most *Larrea* establishment apparently occurs while the *Ambrosia* individuals are alive. The smallest *Larrea*

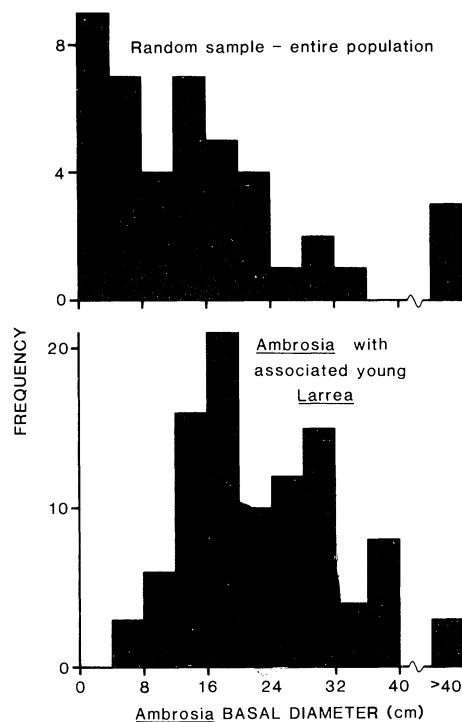


FIG. 1.—Basal diameters of *Ambrosia dumosa* sampled at random from the entire Dateland population (upper histogram) and from individuals with young *Larrea* plants positioned beneath their canopies (lower histogram).

shrubs at Dateland are associated exclusively with live *Ambrosia*. Mortality among *Ambrosia* shrubs with young *Larrea* plants beneath their canopies increases with the average size and estimated age of the associated *Larrea*; a similar pattern occurs at San Luis (table 2).

Unlike young *Larrea* shrubs, most young *Ambrosia* are located in open space away from other plants. At Dateland and San Luis, 83.0% and 91.9%, respectively, of all young *Ambrosia* plants are located in open space. These proportions are nearly equivalent to the fraction of space that is open at each of the two sites (table 1). Distance sampling conducted at Dateland indicates that the positioning of young *Ambrosia* plants is random with respect to the locations of larger, older *Ambrosia* and *Larrea*. The mean distance between 100 young *Ambrosia* shrubs and the nearest living or dead *Ambrosia* ($\bar{X} = 95$ cm, $SD = 59$ cm) is statistically indistinguishable from the mean distance between 40 randomly positioned sample points and the nearest living or dead *Ambrosia* ($\bar{X} = 93$ cm, $SD = 52$ cm; $t = 0.15$, $P > 0.50$). Similarly, the mean distance between the 100 young *Ambrosia* plants and the nearest neighboring *Larrea* ($\bar{X} = 342$ cm, $SD = 168$ cm) does not differ statistically from the mean distance between the 40 randomly positioned points and the nearest *Larrea* ($\bar{X} = 299$ cm, $SD = 165$ cm; $t = 1.37$, $P > 0.10$).

In addition to differences in recruitment location, the two species also differ

TABLE 2

MORTALITY AMONG *AMBROSIA DUMOSA* WITH ASSOCIATED YOUNG *LARREA TRIDENTATA* SHRUBS

Site	Trunk Diameters (mm) of Young <i>Larrea</i> Associated with <i>Ambrosia</i> Canopies		Estimated Age of Young <i>Larrea</i> (yr)	% Mortality among <i>Ambrosia</i> with Associated Young <i>Larrea</i> of Indicated Size
	mm	n		
Dateland	5-9	4	4-8	0
	10-19	23	9-17	43
	20-29	37	18-26	32
	30-39	42	27-35	60
	40-49	13	36-44	77
San Luis	10-19	12	8-14	67
	20-29	11	15-22	73
	30-40	7	23-31	86

considerably in recruitment rates and population turnover. Recruitment of *Larrea* is infrequent. Despite an abundance of potentially suitable areas beneath *Ambrosia*, young *Larrea* shrubs are found beneath only about 1% of all live *Ambrosia* canopies at both sites. Total densities of young *Larrea* shrubs are 15.0 individuals per hectare at Dateland and 12.5/ha at San Luis. Young *Ambrosia* shrubs are nearly 10 times as abundant as young *Larrea* at both sites (123/ha at Dateland; 105/ha at San Luis).

Age estimates based on counts of growth rings in trunk cross sections allowed calculation of average annual recruitment rates. The average interval between growth rings in young *Larrea* (average trunk radius divided by the number of radial growth rings) is 0.56 mm at Dateland (SD = 0.13 mm, $n = 28$) and 0.65 mm at San Luis (SD = 0.17 mm, $n = 14$). These values are similar to the radial growth increments that Vasek (1980) claimed were annual rings in Mojave Desert *Larrea*. The 12-mo record of radial growth obtained from cambium-scarred individuals at Dateland suggests that these rings are annual increments. In each of the nine individuals examined, only one growth ring had formed in a 12-mo period since the date of cambium scarring. The distinct ring apparently arises from the annual cessation of growth during the predictable and extremely dry pre-summer drought of April to June. In the cambium-scarred individuals, radial trunk growth in 1 yr ranged from 0.30 mm to 0.60 mm ($\bar{X} = 0.41$ mm, SD = 0.10 mm). Virtually all of this growth occurred within the first 6 mo following the date of cambium scarring. This period included the winter rainy season. Four cross sections obtained after 6 mo showed radial trunk growth ranging from 0.30 to 0.50 mm ($\bar{X} = 0.39$ mm, SD = 0.09 mm).

Average 12-mo radial growth measured in cambium-scarred individuals (0.41 mm) is slightly less than the 0.56-mm average for growth-ring intervals measured in trunk cross sections of young individuals from Dateland. Since most growth in *Larrea* apparently occurred during the winter rainy season, this slight difference may be due to below-average precipitation that occurred throughout the region in December 1985 and January 1986. Precipitation records are not available for the

TABLE 3

ABUNDANCE OF YOUNG *LARREA TRIDENTATA* SHRUBS BY SIZE AND ESTIMATED AGE CLASS

TRUNK-DIAMETER CLASS (mm)	DATELAND		SAN LUIS	
	Estimated Age Class* (yr)	Absolute Frequency	Estimated Age Class† (yr)	Absolute Frequency
5-10	4-9	9	4-7	1
11-15	10-13	13	8-11	8
16-20	14-18	21	12-15	14
21-25	19-22	16	16-19	8
26-30	23-27	15	20-23	6
31-35	28-31	29	24-27	7
36-40	32-36	17	28-31	5

* Calculated from average radial growth of 0.56 mm/yr.

† Calculated from average radial growth of 0.65 mm/yr.

Dateland site, but during these two normally wet months, each of 14 southwestern Arizona weather stations located within 200 km of Dateland reported below-average precipitation that ranged from 14% to 95% of normal amounts and averaged 55% of normal amounts (NOAA 1985, 1986). Additional evidence for below-average precipitation during the winter of 1985/1986 at the Dateland site was the almost complete lack of a normal late-winter and early-spring ephemeral flora.

For Dateland and San Luis, respectively, I used 0.56 mm and 0.65 mm as estimates of average annual radial growth in estimating the ages of young *Larrea* shrubs on the basis of trunk-diameter measurements. Given these rates of radial growth, young *Larrea* shrubs having basal stem diameters of 5-40 mm would have corresponding ages of approximately 4-36 yr at Dateland and 4-31 yr at San Luis. The densities of young *Larrea* divided by these time intervals (32 and 27 yr) yielded estimated recruitment rates of 0.47 individuals/ha/yr at Dateland and 0.46 individuals/ha/yr at San Luis. Although recruitment in *Larrea* no doubt fluctuates to some extent from year to year (table 3; cf. Ackerman 1979), these estimated rates are indicative of average annual recruitment into the class of young *Larrea* over approximately the last 30 yr.

In cross sections of young *Ambrosia* stems from Dateland (San Luis specimens were not collected), intervals between radial growth rings ranged from 0.88 mm to 1.50 mm (\bar{X} = 1.22 mm, SD = 0.53 mm, n = 11). No cambium-scarring experiment was performed with young *Ambrosia* plants, but I assumed these rings to be annual increments because plants remain leafless and no stem elongation occurs during the hot summer months, despite the occurrence of rains. With an average radial growth rate of 1.22 mm/yr, young *Ambrosia* plants with basal stem diameters of 5-15 mm have estimated ages of 2-6 yr. Since the ages of young *Ambrosia* plants span a 4-yr period, average annual recruitment into the young *Ambrosia* population is estimated at 30.8 individuals/ha at Dateland and 26.3/ha at San Luis.

Differing recruitment rates of the two shrub species were also seen in disturbed areas from which perennial plant cover was removed. An area 125 m by 1000 m situated 2 km from the San Luis study site and originally covered by both *Larrea*

and *Ambrosia* (determined from aerial photographs taken in 1973), was scraped clean of all perennial vegetation around 1975 to prepare an irrigated field. After scraping, the disturbed land was not further developed or used. Data collected in 1985 show that *Ambrosia* has rapidly colonized the disturbed area, but few *Larrea* plants are present. The mean densities of *Ambrosia* and *Larrea* in adjacent undisturbed areas are 11.0 and 0.67 individuals/100 m², respectively. The mean density of *Ambrosia* on the disturbed site is 19.2 individuals/ha, whereas only one *Larrea* individual was included within a 25,000-m² area sampled (0.004 *Larrea* individuals/100 m²). More-rapid colonization of disturbed areas by *Ambrosia* than by *Larrea* has also been reported from sites in the Mojave Desert (Vasek 1979/1980, 1983; Hunter 1987).

In the *Ambrosia* population, a high mortality rate balances the high recruitment rate. In contrast, *Larrea* has a relatively low mortality rate as indicated by the rarity of dead *Larrea* and the abundance of dead *Ambrosia*. Remains of dead *Larrea* plants account for an estimated 10 individuals/ha, or 4.6% of all *Larrea* in the Dateland population. Similarly, dead *Larrea* plants account for only 7.5 individuals/ha at San Luis, or 8.8% of the *Larrea* population. Standing dead *Ambrosia* are far more abundant. Dead individuals account for 52.9% of all *Ambrosia* at Dateland and 55.2% at San Luis (1482 and 663 dead individuals/ha, respectively). To calculate average annual mortality, I divided the density of standing dead stems by the estimated time required for woody remains to decay to a point at which they could no longer be identified to species.

Extremely slow decay of wood in dry environments accounts for an abundance of standing dead individuals. An 11-yr study by Ebert and Zedler (1984) in the Sonoran Desert of southern California revealed that sections of *Fouquieria splendens* stems weighing 1–100 kg required 20–30 yr to lose half their original dry mass through decay; similarly slow rates of decay probably exist for *Larrea* and *Ambrosia* wood at Dateland and San Luis. Decay rates are strongly influenced by precipitation, and at both study sites, annual precipitation totals are similar to those in the area studied by Ebert and Zedler. Wood decomposition can be represented as an exponential decay process (Ebert and Zedler 1984). Because of differences in the density of wood and apparent decay resistance, I estimated an average half-life of 30 yr for *Larrea* and 20 yr for *Ambrosia* for the loss of mass through decay. For both species, I assumed that remains of individuals can be correctly identified after two half-lives have elapsed following death, that is, when only 25% of the original mass remains (60 yr for *Larrea* and 40 yr for *Ambrosia*).

Dead of both species at both sites exhibited various states of decomposition. All dead individuals were assigned to one of four decay categories: I, recently deceased plants that have not lost any small terminal twigs; II, dead plants that have completely lost the smallest twigs; III, plants represented by the standing remains of the central stems and a few main branches; and IV, dead plants that are prostrate on the soil surface but still have fragments of the main stem inserted in the soil. Percentages of dead *Larrea* ($n = 50$) assigned to each of these decay categories are I, 6%; II, 36%; III, 36%; IV, 22%. Percentages of dead *Ambrosia* ($n = 165$) in each category are I, 22%; II, 20%; III, 37%; IV, 21%. Given the length of time required for the decay of woody remains, the presence of individuals in

each of these various stages of decomposition indicates that mortality within both species has been distributed through time and is not the result of any single catastrophic event.

Assuming a 60-yr period for woody remains of *Larrea* to decay beyond the point of recognition, I calculated average mortality of 0.167 and 0.125 deaths per hectare per year for the Dateland and San Luis populations, respectively. Using an estimated decay period of 40 yr for *Ambrosia* remains, I calculated average mortality of 37 deaths per hectare per year at Dateland and 17 deaths per hectare per year at San Luis.

To summarize, these simple plant communities essentially consist of two species having completely different patterns of recruitment and rates of population turnover. The majority of space is devoid of perennial plant cover, and *Ambrosia* readily colonizes this open space. Recruitment of *Larrea* occurs less frequently and is largely limited to areas beneath canopies of large, older *Ambrosia*.

Dynamics

Open space, space covered by *Ambrosia* canopies, and space covered by *Larrea* canopies are more or less discrete states of the occupation of space. Knowledge of the transitions among these states provides a basis for describing dynamics. The predominance of *Larrea* establishment beneath *Ambrosia* canopies followed by the subsequent death of the *Ambrosia* indicates that space initially occupied by *Ambrosia* will occasionally shift to occupancy by longer-lived *Larrea* (depicted by arc 1, fig. 2). The rarity or absence of *Larrea* recruitment in the open and in areas beneath larger, older *Larrea* plants indicates that transitions from open space or older *Larrea* to young *Larrea* are far less likely. The abundance of young *Ambrosia* located in open areas indicates that this species is the principal colonizer of open space (arc 2, fig. 2). New open space can

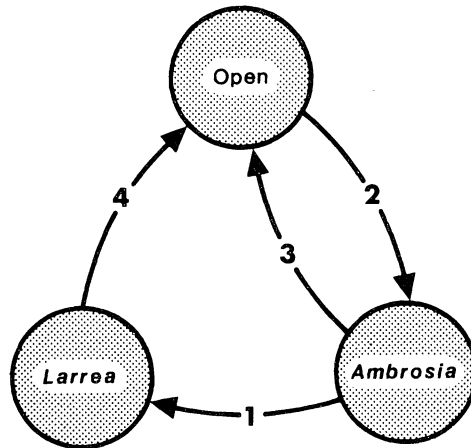


FIG. 2.—Simple digraph showing the principal transitions in the *Larrea*-*Ambrosia* communities at Dateland and San Luis.

arise through the death of individuals of either species (arcs 3 and 4, fig. 2). The consequence of these principal transitions would be a shifting occupation of individual patches, which may be crucial to the maintenance of species codominance. Coexistence of the three states is a qualitative prediction derived from the simple digraph model of this system (fig. 2). The digraph is strongly connected: for every pair of vertices (states) u and v , v can eventually be reached from u and u is reachable from v . Similar underlying dynamics have been suggested for coexistence in simple plant communities in the Chihuahuan Desert (Yeaton 1978; Lozano and Reid 1982), as well as in more-diverse temperate forests (Woods and Whittaker 1981).

The behaviors of these systems resemble regular Markov chains. A Markov chain provides a stochastic model in which the transitions among states occur with characteristic probabilities that depend only on the current state. Markov-chain models have been successfully used to represent dynamics of forest succession (Horn 1975), as well as tree-by-tree replacement patterns underlying steady-state (climax) compositions in forests (Culver 1981). A stochastic model of the dynamics of the Dateland and San Luis plant communities is fitting because the transitions among states are to a large extent inherently probabilistic. For example, despite the abundance of suitable areas beneath large, older *Ambrosia* shrubs where *Larrea* could establish, recruitment actually occurs beneath an extremely small proportion of available *Ambrosia*. Large *Ambrosia* individuals exhibit no obvious differences that might enable a deterministic prediction of which shrubs will foster the recruitment of *Larrea*. Rather, the recruitment of *Larrea* beneath any individual *Ambrosia* canopy can be realistically viewed as an event occurring with a characteristic (albeit small) probability.

In Markovian representations of forest dynamics, the canopies of various species occupying space within a closed canopy have usually been designated as the different states. The dynamics of these systems have been depicted as a tree-by-tree replacement process, in which the probability that species- i canopy tree will be replaced by species- j canopy tree depends only on the frequency of species- j saplings beneath species- i canopy trees. An enumeration of relative frequencies of different species of saplings beneath different species of canopy trees represents the only data needed to generate a matrix of transition probabilities. Transition probabilities for the Dateland and San Luis systems could not be estimated in the same manner because unoccupied space is included as a separate state. The probability of transition from any state to open space cannot be obtained by counting the relative frequency of "young individuals" of open space beneath canopies of various other species. However, estimates of recruitment and mortality rates can be used to calculate transition probabilities on an average annual basis. Transitions were considered as cell-by-cell replacements, in which the size of a cell is equivalent to the area covered by an *Ambrosia* canopy of average size. Data used in calculating these probabilities are listed in table 4; transition matrices for both sites are shown in table 5. The calculations used are detailed below.

The annual per capita probabilities of death in both species are used as esti-

TABLE 4

VARIABLES USED IN CALCULATING TRANSITION PROBABILITIES FOR THE DATELAND AND SAN LUIS SITES

VARIABLE	DEFINITION	ESTIMATED VALUES	
		Dateland	San Luis
<i>A</i>	Number of dead <i>Ambrosia</i> /ha	1482	663
<i>B</i>	Number of live <i>Ambrosia</i> /ha	1321	538
<i>C</i>	Estimated number of years after death required for <i>Ambrosia</i> to decay beyond recognition	40	40
<i>D</i>	Number of dead <i>Larrea</i> /ha	10.0	7.5
<i>E</i>	Number of live <i>Larrea</i> /ha	207.7	77.5
<i>F</i>	Estimated number of years after death required for <i>Larrea</i> to decay beyond recognition	60	60
<i>G</i>	Average recruitment of young <i>Ambrosia</i> in open space (number/ha/yr)	30.8	26.3
<i>H</i>	Arbitrary cell size = the area covered by an average <i>Ambrosia</i> canopy (m ²)	.449	.468
<i>I</i>	Number of <i>Ambrosia</i> -sized cells of open space/ha	19532	20235
<i>J</i>	Recruitment of young <i>Larrea</i> in the open (number/ha/yr)	.048	.150
<i>K</i>	Area covered by average <i>Larrea</i> canopy (m ²)	2.755	3.550
<i>L</i>	Number of <i>Ambrosia</i> -sized cells of open space eventually covered by a single <i>Larrea</i> canopy (= K/H)	6.14	7.59
<i>M</i>	Recruitment of <i>Larrea</i> beneath <i>Ambrosia</i> (number/ha/yr)	.402	.310
<i>N</i>	Average number of cells of open space eventually covered by canopy of <i>Larrea</i> that originally established beneath a single <i>Ambrosia</i> (= $L - 1$)	5.14	6.59

mates of the probabilities that space occupied by canopies of these species will revert to open space through mortality (p_{21} and p_{31} in the transition matrices). The variables used to compute these probabilities are the densities of live and dead individuals and the estimated lengths of time required after death for the woody remains to decay beyond recognition (table 4: variables *A*, *B*, and *C* for *Ambrosia* and *D*, *E*, and *F* for *Larrea*). For either species, this probability, p , could be computed from the relationship $lpg = d$, where l is the density of live individuals; p , the annual per capita probability of death; g , the years required for decay of woody remains; and d , the density of identifiable remains of dead individuals.

The probability that open space will become occupied by *Ambrosia* (p_{12}) is calculated by dividing the estimated annual recruitment for the *Ambrosia* population by the number of *Ambrosia*-sized cells of open space per hectare (G/I in table 4). Since the direct transition from canopy cover of *Larrea* to canopy cover by *Ambrosia* does not occur, a value of zero is assigned to p_{32} .

The probability p_{13} , the likelihood that a cell of open space will be covered by *Larrea*, has two components. For each *Larrea* plant colonizing open space, an equivalent of more than six *Ambrosia*-sized cells of open space will eventually be covered because of the greater size of *Larrea* canopies. By using variable names listed in table 4, this component of the transition from open space to cover by

TABLE 5

MATRICES (**P**) OF TRANSITION PROBABILITIES FOR THE DATELAND AND SAN LUIS SYSTEMS

Present states (<i>i</i>)	Future states (<i>j</i>)			
	Open	<i>Ambrosia</i>	<i>Larrea</i>	
Open (1)	p_{11}	p_{12}	p_{13}	P
<i>Ambrosia</i> (2)	p_{21}	p_{22}	p_{23}	
<i>Larrea</i> (3)	p_{31}	p_{32}	p_{33}	
	$\begin{bmatrix} .99828 \\ .028 \\ .00080 \end{bmatrix}$	$\begin{bmatrix} .0016 \\ .97171 \\ 0 \end{bmatrix}$	$\begin{bmatrix} .00012 \\ .00030 \\ .99920 \end{bmatrix}$	P_{Dateland}
	$\begin{bmatrix} .99854 \\ .031 \\ .0016 \end{bmatrix}$	$\begin{bmatrix} .0013 \\ .96842 \\ 0 \end{bmatrix}$	$\begin{bmatrix} .00016 \\ .00058 \\ .9984 \end{bmatrix}$	P_{San Luis}

Larrea is computed as JL/I , or the density of young *Larrea* plants recruiting in open space multiplied by the number of cells eventually occupied by a *Larrea* canopy divided by the total number of open cells per hectare.

Because the area covered by a single *Larrea* canopy exceeds the coverage of an individual *Ambrosia* canopy by more than a factor of six, colonization of young *Larrea* plants beneath *Ambrosia* canopies results in a second means by which open space is eventually covered by *Larrea* canopies. By using the variables from table 4, the probability of the loss of open space through this process is obtained as the product of M and N divided by I , where M is the recruitment of young *Larrea* plants beneath the *Ambrosia* canopy; N , the number of *Ambrosia*-sized cells of open space eventually covered by a *Larrea* canopy in addition to the single cell originally occupied by *Ambrosia*; and I , the total density of *Ambrosia*-sized cells of open space. The two parts of the probability of transition from open space to *Larrea* canopy cover are summed to yield the probability p_{13} .

The probability of transition from *Ambrosia* to *Larrea* canopy (p_{23}) is obtained by dividing the estimated recruitment of *Larrea* beneath *Ambrosia*, M , by the density of *Ambrosia*, B .

The diagonal values (p_{11} , p_{22} , p_{33}) represent the probabilities that cells in a given state at time t will remain in that state for an additional year. For each of the three states, the annual survival rate equals one minus the sum of the two other probabilities from the corresponding row.

Whereas the transition matrices are intended to represent probabilities of annual change, complete transitions in this system actually occur over periods exceeding 1 yr. For example, the local replacement of *Ambrosia* by *Larrea* may take several decades. However, as a necessary simplification in the three-state Markov-chain model, recruitment of a young *Larrea* plant beneath an *Ambrosia* canopy (the survival of a *Larrea* for at least 4 yr following germination) is considered a transition from *Ambrosia* to *Larrea*. This is a reasonable assumption

because most mortality in *Larrea* occurs during the first 1 or 2 yr (Sheps 1973). Small *Larrea* seedlings subject to high mortality were not included in the surveyed "young individual" class. Despite intensive searching at both sites, I found no dead young *Larrea* plants (5–40 mm in basal trunk diameter). This indicates that once small plants attain this size and corresponding age (4+ yr), the probability that they will continue to develop into fully mature plants is close to unity. Similarly, I considered an *Ambrosia* seedling surviving in open space for 2 yr following germination a recruit in the young *Ambrosia* population, hence bringing about a transition of a cell of open space to occupation by *Ambrosia*. These simplifications are preferable at this point to the greater complexity that would result from the inclusion of additional, intermediate states.

Although the values for recruitment and mortality, and hence the derived transition probabilities, are crude estimates, the transition matrices for the Dateland and San Luis systems are strikingly similar for particular p_{ij} 's (table 5). The diagonal values represent probabilities of patches in a given state remaining in that state for an additional year and are the largest probabilities within the matrices. As such, they indicate the near-static condition of these communities in terms of annual change. The values for p_{11} (the likelihood that unoccupied space will remain unoccupied an additional year) and p_{33} (the likelihood that space covered by *Larrea* will remain so for an additional year) represent the largest of the three diagonal values. These large probabilities realistically reflect the slow colonization of open space by perennials, as well as the great longevity of individual *Larrea* plants. The relatively lower value of p_{22} reflects the greater turnover within the population of the shorter-lived *Ambrosia*.

Calculations of average longevity of *Larrea* and *Ambrosia* using mortality data from the transition matrices provide an independent means of examining the degree to which the values for p_{21} and p_{31} realistically reflect mortality rates. Average annual mortality rate can be simply represented as the inverse of longevity, $L = 1/m$, where L is longevity in years and m is annual mortality rate (Acevedo 1981). The transition probabilities p_{21} and p_{31} are estimates of m for *Ambrosia* and *Larrea*, respectively. Average longevity of *Ambrosia* of 35.7 yr at Dateland and 32.3 yr at San Luis are calculated in this manner. Calculated longevity of *Larrea* are 1250 yr at Dateland and 625 yr at San Luis. Although studies of longevity of *A. dumosa* have not been published, long-term studies of the similar congener *A. deltoidea* in the Sonoran Desert suggest average longevity somewhat less than 50 yr (Goldberg and Turner 1986). *Larrea* attain ages much greater than this; individuals at some sites may live several thousand years. Vasek (1980) reported estimates of radial basal growth of 0.52 mm/yr in *L. tridentata* clones from the Mojave Desert. Given this rate of radial growth, the largest living individuals at Dateland and San Luis with basal diameters of 192 cm and 157 cm, respectively, would have corresponding ages of 1846 yr and 1510 yr. The mean basal diameter of all live *Larrea* at Dateland was 36 cm (SD = 41.1 cm) and at San Luis 39 cm (SD = 37.8 cm). Corresponding estimated ages for *Larrea* within the two populations are 346 yr and 375 yr, representing a lower estimate of average longevity. The mean basal diameters of dead individuals at Dateland and San Luis were 40.8 cm (SD = 21.3) and 43.3 cm (SD = 12.2). These sizes

correspond to estimated ages of 392 yr and 416 yr when death occurred. The longevities for *Larrea* calculated as the inverse of estimated mortality are intermediate between low and high estimates of longevities based on estimated basal growth rates. The general agreement between these independently calculated longevities suggests that the values for p_{31} are reasonable.

In terms of changes in species composition, these simple plant communities probably represent some of the most stable assemblages in the Sonoran Desert. Because these areas lack economic value, neither of the study sites has experienced a history of extreme disturbances brought about by grazing or other activities associated with the more recent human settlement of the Southwest. Radiocarbon-dated plant fossils from packrat middens indicate that *A. dumosa* and *L. tridentata* have coexisted in the general geographic area of the sites since at least the end of the last glacial period approximately 11,000 yr ago (Van Devender et al., in press). Assuming that the compositions of the Dateland and San Luis communities have been relatively stable for an extended period of time, I now address the question of whether the Markov-chain model of dynamics predicts coexistence of the two species, as well as equilibrium compositions similar to those observed.

In the Markov-chain model, the relative proportions, n_i , of the three states of space occupancy are represented as a state vector, \mathbf{N} :

$$\mathbf{N} = (n_1, n_2, n_3). \quad (1)$$

This vector representing the distribution of states at time t multiplied by the transition matrix \mathbf{P} yields the distribution of states at time $t + 1$:

$$\mathbf{N}(t)\mathbf{P} = \mathbf{N}(t + 1). \quad (2)$$

This new value of \mathbf{N} can then again be multiplied by \mathbf{P} to yield the distribution of states at the end of the next time interval, and so on. For a regular Markov chain, the distribution of states in \mathbf{N} will eventually reach a stationary distribution that is determined by the values of p_{ij} in \mathbf{P} but is independent of the initial distribution of states in \mathbf{N} . This stationary distribution of states is called the steady-state vector, \mathbf{N}^* , of the transition matrix \mathbf{P} . If such a vector \mathbf{N}^* exists, it is the solution of the equation

$$\mathbf{N}^* = \mathbf{N}^*\mathbf{P}, \quad (3)$$

where additional multiplication of \mathbf{N} by the transition matrix yields no further change in the distribution of states. For the Markov chain with three states presented here, equation (3) is equivalent to a system of three linear equations:

$$\begin{aligned} n_1 &= n_1p_{11} + n_2p_{21} + n_3p_{31}, \\ n_2 &= n_1p_{12} + n_2p_{22} + n_3p_{32}, \\ n_3 &= n_1p_{13} + n_2p_{23} + n_3p_{33}. \end{aligned} \quad (4)$$

In calculating the stationary distribution of states in terms of the proportion of space occupied by each state, \mathbf{N}^* is treated as a probability vector where the solution to the equations in (4) must also satisfy the relationship $\sum n_i = 1$.

TABLE 6

OBSERVED RELATIVE FREQUENCIES OF THE THREE COVER TYPES AT DATELAND AND SAN LUIS
AND THE STATIONARY DISTRIBUTION OF STATES PREDICTED FROM THE MATRICES
OF TRANSITION PROBABILITIES IN TABLE 5

COVER TYPE	DATELAND*		SAN LUIS	
	Observed	Predicted	Observed	Predicted
Open	.883	.814	.947	.865
<i>Ambrosia</i>	.057	.046	.025	.036
<i>Larrea</i>	.059	.139	.028	.099

* Proportions do not add to 1.000 on account of a rounding error.

The stationary distributions of states for the Dateland and San Luis communities predicted from the transition matrices are similar to the observed distributions of states (table 6). The three-state Markov-chain model not only predicts codominance of the two species, it predicts that the majority of space will remain devoid of canopy cover. Both chains, however, predict a slightly greater amount of cover of *Larrea* than actually observed. The relative difference between the Dateland and San Luis sites in terms of the amount of space lacking canopy cover is a feature more accurately depicted. Although simple, this Markovian representation realistically encapsulates important features of the behaviors of each species that ultimately contribute to coexistence.

Homogeneous or Nonhomogeneous Chains?

The model as presented is a homogeneous Markov chain, in which the transition probabilities are independent of the values of n_i and are therefore constant over time. The transition probabilities for the Dateland and San Luis systems (table 5) are based on measurements within undisturbed, presumably stable communities. If the distribution of states in either of these systems were greatly displaced from a stationary distribution, these fixed probabilities might not accurately predict subsequent rates of compositional change. The dynamics of the Dateland and San Luis systems might be more accurately modeled as nonhomogeneous Markov chains in which transition probabilities vary as a function of changing values of n .

The homogeneous Markov chain using fixed transition probabilities for the San Luis site listed in table 5 predicts that completely denuded areas will be colonized far more rapidly by *Ambrosia* than by *Larrea* (fig. 3), but the predicted rate of colonization by *Ambrosia* is slower than the rate observed in the disturbed site. According to the homogeneous Markov-chain model, approximately 100 yr elapse before *Ambrosia* cover approaches equilibrium values; a peak is not reached until 186 yr (fig. 3). Yet, on the disturbed site, *Ambrosia* densities exceeding those of undisturbed areas were reached within a decade. This discrepancy is most likely due to density-dependent changes in recruitment and mortality. Recruitment of *Ambrosia* eventually declines and mortality increases as functions of increased densities of conspecifics and *Larrea*. Such density-dependent changes in transi-

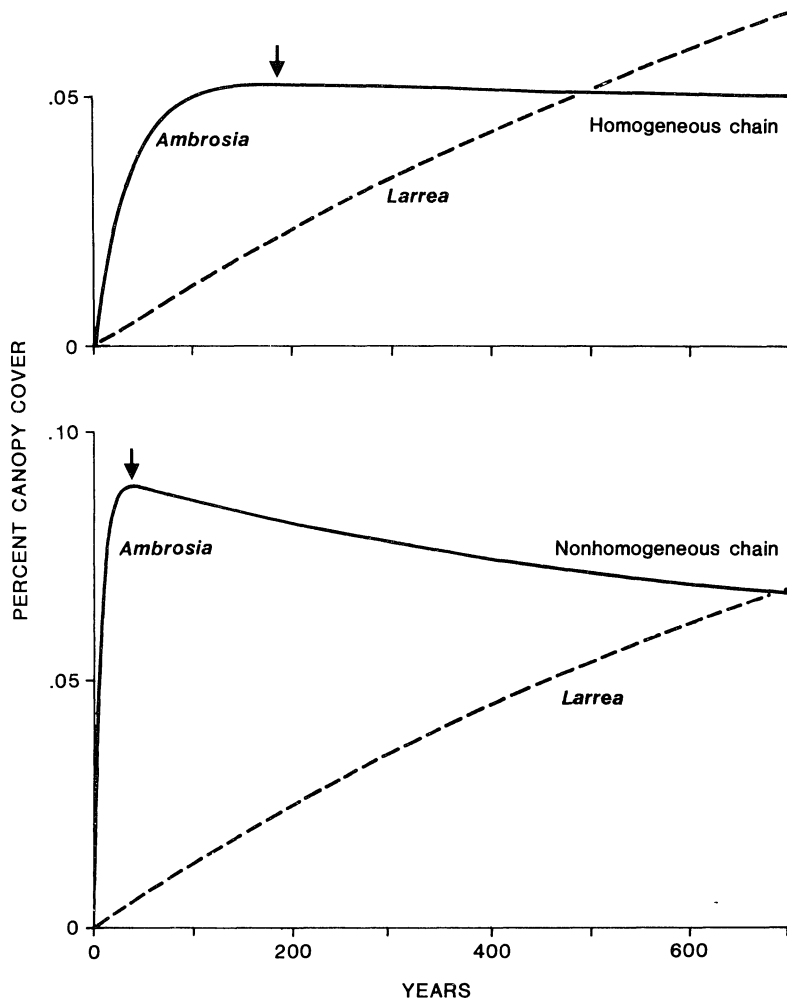


FIG. 3.—Projected distributions of cover by *Ambrosia* and *Larrea* predicted from homogeneous (top) and nonhomogeneous (bottom) Markov-chain models. Arrows, Peaks in the abundance of *Ambrosia*.

tion probabilities can be incorporated within a nonhomogeneous Markov-chain model (Acevedo 1981).

Recruitment rates of *Ambrosia* during the initial colonization of completely denuded areas far exceed recruitment within undisturbed areas inhabited by both *Ambrosia* and *Larrea*. In other words, the value of p_{12} would be greater at low densities of *Ambrosia* and *Larrea* than at high densities. As discussed earlier, recolonization of completely denuded areas by *Ambrosia* is extremely rapid. Within 10 yr following removal of all vegetation in the disturbed area at San Luis, the *Ambrosia* population has reached a density of 1920 individuals per hectare, nearly twice that of adjacent undisturbed areas. Estimated annual recruitment

over the first decade of recolonization is therefore 192 *Ambrosia* per hectare per year, over seven times the estimated annual recruitment in undisturbed areas (table 4). Within the newly colonized disturbed area, the mortality rate for *Ambrosia* is lower than that within undisturbed areas. Of 231 *Ambrosia* individuals counted within 12 100-m² plots in the disturbed area, only one was dead. The estimated mortality rate of *Ambrosia* during the initial 10 yr of recolonization is therefore 0.043% per year. The estimated *Ambrosia* mortality rate within adjacent undisturbed areas is approximately 70 times this value, or 3.12% per year (table 5). This great difference in mortality rate may be attributable not only to density-dependent effects, but also, in part, to changes in the age structure of the *Ambrosia* population. Disturbed areas that have been recently colonized would contain only young plants, whereas undisturbed communities would have a larger proportion of senescent individuals. Nevertheless, mortality rate undoubtedly increases through time following the initial stages of colonization as densities of both species increase.

Using the above data, I considered recruitment and mortality as linear functions of the combined cover of *Ambrosia* and *Larrea*. I calculated that maximum *Ambrosia* recruitment (192/ha/yr) occurs when canopy cover is completely absent, decreases linearly to 26.3/ha/yr when cover values reach 5.3%, and continues to decrease linearly for cover values exceeding 5.3%. The value 5.3% represents the percentage of canopy cover in undisturbed areas at San Luis. Mortality rate was calculated as increasing linearly from a minimum of 0.043%/yr at the earliest stages of colonization to 3.1%/yr when total cover reached 5.3%. These calculations, performed at every iteration of the Markov chain, yielded the values required for computing the changing values of p_{12} and p_{21} in a nonhomogeneous Markov chain.

The nonhomogeneous chain predicts that colonization of *Ambrosia* will be far more rapid than predicted by the homogeneous Markov chain (fig. 3). In the nonhomogeneous chain, the rapid colonization of *Ambrosia* results in *Ambrosia* cover approaching equilibrium values within 10–15 yr, as actually observed at San Luis. The nonhomogeneous chain also predicts that *Ambrosia* cover will initially exceed equilibrium values, reach a peak at 36 yr, and then decline slowly as the abundances of both *Ambrosia* and *Larrea* increase. This prediction qualitatively agrees with the observation that the density of *Ambrosia* 10 yr after the disturbance exceeds densities in adjacent, undisturbed areas.

RESULTS: SPECIES-RICH ASSEMBLAGES

Recruitment Patterns

Species-rich communities in bajada habitats contain a variety of plant life forms including small trees, shrubs, and succulents. The three sites positioned along the bajada gradient at Saguaro National Monument exhibit declines in canopy cover and species richness from upper to lower sites similar to those described for such gradients by other authors (Yang and Lowe 1956; Solbrig et al. 1977). Despite these declines, at each of these sites young individuals of most perennial species

TABLE 7

PATTERNS OF RECRUITMENT OF VARIOUS TREES, SHRUBS, AND SUCCULENTS ALONG A BAJADA GRADIENT

BAJADA LOCATION AND SPECIES OF YOUNG INDIVIDUALS*		COVER TYPE		
		Open	<i>Ambrosia deltoidea</i>	Other Plants
UPPER BAJADA				
Proportion of cover		(.510)	(.340)	(.150)
Shrubs				
<i>Ambrosia deltoidea</i> ^a	49	.857 (+)	.143 (-)	0
<i>Larrea tridentata</i> ^b	50	.360 (-)	.640 (+)	0
<i>Fouquieria splendens</i> ^b	50	.040 (-)	.780 (+)	.180
<i>Jatropha cardiophylla</i> ^c	30	.233 (-)	.600 (+)	.167
<i>Krameria</i> sp. ⁱ	24	.333 (-)	.625 (+)	.042
Tree				
<i>Cercidium microphyllum</i> ^b	24	.042 (-)	.958 (+)	0
Succulents				
<i>Opuntia acanthocarpa</i> ^d	50	.040 (-)	.960 (+)	0
<i>O. phaeacantha</i> ^e	45	.044 (-)	.911 (+)	.044
<i>O. fulgida</i> ^f	11	.727	.273	0
<i>Ferocactus wislizenii</i> ^g	17	.235	.529 (+)	.236
<i>Carnegiea gigantea</i> ^h	14	0	.929 (+)	.071
<i>Echinocereus fasciculatus</i> ⁱ	14	.142 (-)	.429 (+)	.429
<i>Mammillaria microcarpa</i> ⁱ	18	0 (-)	.389 (+)	.661
MIDDLE BAJADA				
Proportion of cover		(.540)	(.350)	(.110)
Shrubs				
<i>Ambrosia deltoidea</i> ^a	116	.914 (+)	.017 (-)	.069
<i>Larrea tridentata</i> ^b	28	.321 (-)	.643 (+)	.036
<i>Fouquieria splendens</i> ^b	15	0 (-)	.800 (+)	.200
Succulents				
<i>Opuntia acanthocarpa</i> ^d	35	0 (-)	.943 (+)	.057
<i>O. phaeacantha</i> ^e	30	.067 (-)	.900 (+)	.033
<i>O. leptocaulis</i> ^h	38	.079 (-)	.737 (+)	.148
<i>O. fulgida</i> ^f	12	.750	.167	.083
LOWER BAJADA				
Proportion of cover		(.717)	(.167)	(.166)
Shrubs				
<i>Ambrosia deltoidea</i> ^a	111	.784	.027	.189
<i>Larrea tridentata</i> ^b	50	.360 (-)	.640 (+)	0
Succulents				
<i>Opuntia acanthocarpa</i> ^d	24	0 (-)	.917 (+)	.083
<i>O. phaeacantha</i> ^e	9	0 (-)	1.000 (+)	0
<i>O. fulgida</i> ^f	43	.721	.186	.093

NOTE.—Data presented are the relative frequencies of young individuals associated with each cover type. (+) indicates significant positive associations; (-) indicates significant negative associations (χ^2 goodness-of-fit tests, $P < 0.05$). The positioning of the symbol (+) midway between proportions indicates a pooling of data for the two cover types.

* Superscripts indicate species in which individuals were designated young according to the following arbitrary size criteria: *a*, basal stem diameter 5–15 mm; *b*, basal stem diameter 5–50 mm; *c*, less than 10 basal stems and root crown diameter < 10 cm; *d*, basal stem diameter < 20 mm; *e*, plants with internode number < 15; *f*, height 15–30 cm; *g*, height < 30 cm; *h*, height < 100 cm; *i*, all individuals included.

are found beneath canopies of other plants and especially beneath canopies of *Ambrosia deltoidea*. Recruitment of most species rarely occurs in the open. Young *A. deltoidea* plants, however, are commonly found in open areas, and at two of the three sites they are negatively associated with areas covered by canopies of older, larger *A. deltoidea* shrubs or other species (table 7).

With the predominance of recruitment of most plants beneath *A. deltoidea*, temporal sequences of the occupation of space by different species appear to be one of the principal components of the dynamics of the species-rich assemblages. Additional evidence corroborates such sequences. The general absence of associations between younger, smaller *A. deltoidea* plants and other perennials indicates that *A. deltoidea* is generally the first occupant of a patch and is only later followed by other species. Young individuals of various perennials are associated with larger, presumably older *A. deltoidea* individuals. Of 103 *A. deltoidea* plants lacking associated perennials, 82 were 5 cm or less in root crown diameter. However, only 2 of 101 *A. deltoidea* plants that had other perennials positioned beneath their canopies had basal diameters 5 cm or less ($\chi^2 = 127$, $P \ll 0.001$). Although the youngest individuals of most perennials are associated with living *A. deltoidea* plants, perennials of intermediate size are often found next to dead *A. deltoidea* individuals. The largest members of these populations of various perennial species usually show no trace of a neighboring *A. deltoidea* because they presumably have long outlived any *A. deltoidea* plants that originally fostered their establishment (fig. 4). In species with average longevities far exceeding that of *A. deltoidea*, such as the tree *Cercidium microphyllum*, most individuals within the population are larger and older and bear no evidence of former associations with *A. deltoidea* or other species, even though all smaller individuals show such associations. In perennials presumed to have relatively shorter life spans, such as *Opuntia acanthocarpa* (see longevity data for the similar *O. versicolor* in Goldberg and Turner 1986), far fewer individuals outlive the individual *Ambrosia* beneath which they initially established (fig. 4).

These establishment patterns and resulting temporal sequences in the occupation of space are widespread in bajada and other non-mountainous habitats in the Sonoran Desert. In the Central Gulf Coast vegetational subdivision at Punta Chueca, Sonora, Mexico, most recruitment of the two dominant tree species (*Bursera microphylla* and *C. microphyllum*), as well as the predominant shrub species (*Fouquieria splendens*, *Jatropha cinerea*, and *J. cuneata*), occurs beneath canopies of the shrub *A. dumosa* (table 8; McAuliffe 1986). Humphrey (1974, pp. 96–98) documented that most recruitment of the boojum, *Idria columnaris*, in Baja California, Mexico, occurs beneath shrubs, especially *A. magdalenae*. Many other studies have documented the importance of existing canopy cover for the establishment of various other Sonoran Desert trees, shrubs, and succulents (Turner et al. 1966; Sherbrooke 1977; Steenbergh and Lowe 1977; Jordan and Nobel 1979; McAuliffe 1984b). Similar establishment patterns of perennials have also been documented in the Mojave Desert (Vasek 1979/1980, 1983; Wallace and Romney 1980), the Chihuahuan Desert (Yeaton 1978; Lozano and Reid 1982; Yeaton and Manzanares 1986), and in other semidesert regions of the world, such as the Karoo of South Africa (Compton 1929).

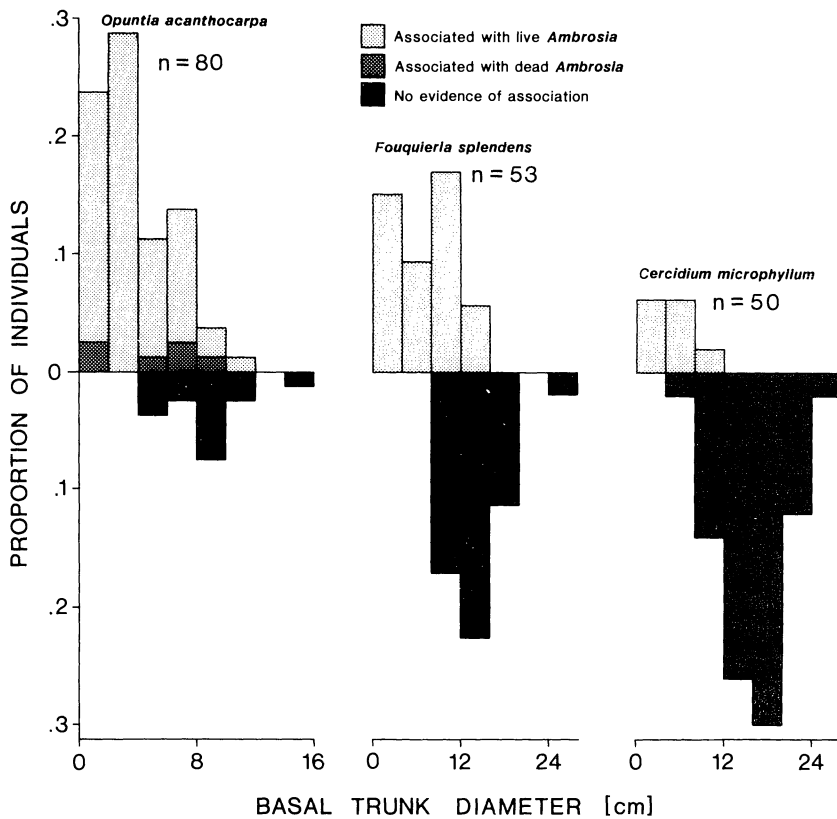


FIG. 4.—The association of three perennial species with canopies of *Ambrosia deltoidea* as a function of basal trunk diameter (relative age).

Dynamics

The recruitment and replacement patterns observed within species-rich communities (tables 7, 8) are similar to those seen in the simple Dateland and San Luis communities. I suggest that these multi-species communities exhibit qualitatively similar dynamics. These species-rich communities consist of the same basic states of the occupation of space: (1) open space, (2) space covered by a species apparently capable of establishing in the open (often *Ambrosia* spp. in the Sonoran Desert), and (3) a diverse suite of other perennial species for which recruitment is largely limited to space beneath *Ambrosia* or other plant canopies. These three states and the principal transitions among them could result in a system with dynamics similar to those portrayed in figure 2.

Such a representation of dynamics for the species-rich systems is an extreme oversimplification, in part because of other replacement sequences involving species pairs of which *Ambrosia* is not a member. For example, in upper-bajada communities in the Sonoran Desert, virtually all recruitment of the tree *Cercidium*

TABLE 8

DISTRIBUTIONS OF YOUNG INDIVIDUALS OF PERENNIAL SPECIES WITH RESPECT TO AVAILABLE COVER:
CENTRAL GULF COAST VEGETATION OF PUNTA CHUECA, SONORA, MEXICO

PERENNIAL PLANT COVER	RELATIVE FREQUENCY	RELATIVE FREQUENCY OF YOUNG INDIVIDUALS IN EACH COVER TYPE				
		TREES		SHRUBS		
		<i>B. micro- phylla</i> (n = 37)	<i>C. micro- phyllum</i> (n = 46)	<i>J. cinerea</i> (n = 7)	<i>J. cuneata</i> (n = 10)	<i>F. splendens</i> (n = 11)
None	.651	.027 (-)	.022 (-)	0 (-)	0 (-)	0 (-)
<i>Ambrosia dumosa</i>	.065	.514 (+)	.609 (+)	.714	.800 (+)	1.000 (+)
<i>Bursera microphylla</i>	.069	.135	.217	0	.200	0
<i>Cercidium microphyllum</i>	.059	.162	0	0	0	0
<i>Jatropha cinerea</i>	.037	0	.022	0	0	0
<i>J. cuneata</i>	.034	.108	.022	.286	0	0
<i>Fouquieria splendens</i>	.015	0	0	0	0	0
Others (8 spp.)	.070	.054	.109	0	0	0

NOTE.—Plus and minus signs indicate significant positive or negative associations (χ^2 tests, $P < 0.05$). Young individuals are arbitrarily defined as follows: *B. microphylla*, <10 cm in basal trunk diameter; *C. microphyllum*, <7.5 cm in basal trunk diameter; *J. cinerea*, <5 stems; *J. cuneata*, <10 basal stems and <10 cm in root crown diameter; *F. splendens*, <5 cm in basal diameter.

microphyllum occurs beneath canopies of *Ambrosia* species (table 7; McAuliffe 1986). In turn, substantial recruitment of the sahuaro cactus, *Carnegiea gigantea*, occurs beneath canopies of *Cercidium microphyllum* (Turner et al. 1966; Steenbergh and Lowe 1977; Nobel 1980; Hutto et al. 1986). Establishment of *Carnegiea* is limited to years with favorable rainfall (Jordan and Nobel 1982), but recruitment beneath any particular tree canopy probably is highly stochastic. Although the numbers of sahuaros associated with a tree of certain size or age might not be deterministically predicted, the likelihood that a tree possesses at least one associated sahuaro increases with tree age, as does the average number of associated sahuaros (table 9). As a result of this process of accumulation of *Carnegiea*, few trees ever "escape" having sahuaros colonize the areas beneath their canopies. The location of sahuaros beneath a tree has deleterious consequences for the tree. Within any size class of *Cercidium*, trees with associated sahuaros suffer higher mortality than trees without associated sahuaros; the cacti almost always outlive the tree (Vandermeer 1980; McAuliffe 1984a). Hence, the *Cercidium*–*Carnegiea* sequence is a highly probable outcome of the initial *Ambrosia*–*Cercidium* sequence. A model incorporating these transitions contributes to a more realistic picture of the dynamics of a species-rich Arizona Upland community (fig. 5). Although seemingly more complex, this digraph model possesses the same qualitative properties of the simple three-state system represented in figure 2 because no absorbing states exist and every state can eventually reach every other state.

TABLE 9

THE ACCUMULATION OF SAHUARO CACTI BENEATH CANOPIES OF
CERCIDIUM MICROPHYLLUM TREES WITH INCREASING AGE OF THE TREE

Basal Diameter of Tree Trunk (cm)	Proportion of Trees with at Least One Sahuaro beneath Canopy	Mean No. of Associated Sahuaros	Tree Sample Size
≤ 10	0	0	2
10.1–20.0	0.23	0.33	30
20.1–30.0	0.64	0.97	58
> 30.0	0.83	1.17	6

NOTE.—Data were collected in March 1983 at Organ Pipe Cactus National Monument, Arizona.

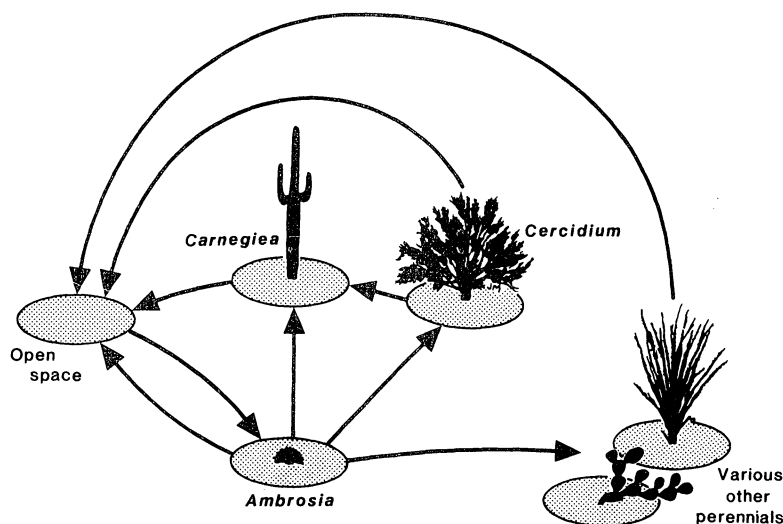


FIG. 5.—Digraph model showing some of the principal transitions among states in a species-rich Arizona Upland plant community.

UNDERLYING MECHANISMS

My descriptions of dynamics have to this point lacked a discussion of causal mechanisms. An initial characterization of the dynamics of these desert plant communities is crucial because it provides a framework that facilitates the formulation of relevant hypotheses concerning underlying mechanisms. Use of a stochastic Markov-chain model does not imply a "random" assembly of these communities; nor does its use indicate an absence of any particular mechanism in driving these dynamics. Although processes such as recruitment within particular microhabitats may be highly stochastic, organization of the community is clearly far from random with respect to differences in recruitment among microhabitats. I review what is known about the mechanisms responsible for these various pat-

terns of recruitment and mortality in desert plant communities. These mechanisms include a variety of physical factors as well as biological interactions among species.

Mechanisms That Permit Recruitment beneath Other Plants

The establishment of certain perennials beneath the canopies of others is one of the principal components of the dynamics of these desert plant communities. The mosaic of shrub canopies and open areas presents physical microhabitats that differ considerably with respect to factors influencing seed distribution, germination, and post-germination survival. Any single factor or combination of factors may facilitate establishment beneath canopies of other plants.

Seed distribution and germination.—Recruitment of certain plants beneath canopies of others may occur because of the accumulation of seeds beneath canopies. Desert plants are often obstructions that result in the deposition of wind- or water-transported seeds beneath their canopies. Agnew and Haines (1960) suggested that this process was responsible for the location of many herbaceous species beneath canopies of perennials in the Iraqi desert. Seed dispersal by animals may also contribute to these recruitment patterns. Yeaton (1978) suggested that bird dispersal of seeds is one factor leading to the establishment of the cactus *Opuntia leptocaulis* beneath canopies of *Larrea tridentata* in the Chihuahuan Desert. Dispersal of seeds by frugivorous birds apparently is a principal factor leading to the common establishment of the sahuaro cactus beneath canopies of trees in the Sonoran Desert (Hutto et al. 1986). In addition to nonrandom seed distribution patterns, the accumulation of fine, windblown material beneath shrub canopies may enhance germination, while the bare desert pavement between shrubs may inhibit successful germination (Wallace and Romney 1980).

Post-germination mortality.—Although patterns of seed distribution and germination may contribute to greater establishment beneath shrub canopies, post-germination mortality undoubtedly limits recruitment in some species. The vulnerability of seedlings to attack by mammals is one factor that eventually restricts young individuals of some plant species to areas beneath plant canopies. Sherbrooke (1977) reported that the majority of germination of the shrub *Simmondsia chinensis* occurred in the open, but subsequent consumption of seedlings by mammals was greater in open areas than in protected areas beneath other plants. Associations of the cactus species *Mammillaria microcarpa* and *Echinocereus engelmannii* with other perennials were attributed in part to similar nonrandom patterns of herbivory (McAuliffe 1984b). In a study of factors limiting recruitment of the tree *Cercidium microphyllum*, the proportion of newly germinated seedlings found in the open (72%) was nearly equivalent to the relative frequency of open space lacking perennial cover (67.3%; McAuliffe 1986). Within the first year, however, a greater proportion of seedlings in the open was consumed by rabbits (*Lepus* spp. and *Sylvilagus audubonii*) than were seedlings positioned beneath *Ambrosia deltoidea*. This pattern of herbivory explains the restricted distribution of older *Cercidium* saplings to areas beneath canopies of other plants, despite a more random distribution of seedlings. *Ambrosia* species may be particularly

effective in concealing seedlings because of their dense, low-lying canopies. Other shrub species, such as *Larrea tridentata* and *Jatropha*, provide far less concealment because of the open character of their canopies and basal stems.

Predation on seedlings may be largely responsible for restricting the distribution of young *Larrea* shrubs to areas beneath canopies of *Ambrosia* at the Dateland and San Luis sites, as well as in communities that have greater numbers of species. Newly germinated *Larrea* seedlings are commonly found in the open, away from other plant canopies. In February and March 1978, following abundant germination, locations of 124 *Larrea* seedlings and the positions of all perennial plant canopies were mapped in eight study plots (10 × 10 m; area B of Shreve and Hinckley 1937; Goldberg and Turner 1986) located on the grounds of the Tumamoc Hill Desert Laboratory at Tucson (unpubl. maps and data provided by Turner). Within these plots, 77.4% of all *Larrea* seedlings were located in open microhabitats. Similarly, in October 1985, I observed that newly emerged *Larrea* seedlings (cotyledon stage only) were common in open microhabitats at the San Luis study site. Jackrabbits (*Lepus* spp.) commonly browse stems of adult *Larrea* (Jaeger 1948; Valentine and Gerard 1968; Chew and Chew 1965; Hunter et al. 1980; pers. obs. at Dateland and San Luis). Boyd and Brum (1983) reported a high incidence of predation, apparently by jackrabbits, on transplanted *Larrea* seedlings at a Mojave Desert site. Although Boyd and Brum concluded that "distance from mature shrubs does not influence rates of seedling predation," their data (1983, p. 30, table 5) show that within 1 mo of transplanting, 33% of 48 seedlings located away from shrub canopies suffered herbivore damage, but only 13% of 24 seedlings transplanted beneath adult *Larrea* were damaged by rabbits. This difference in proportions is marginally significant ($0.05 < P < 0.10$). Furthermore, it is very likely that the above conclusion of Boyd and Brum represents a type-II statistical error resulting from small sample size.

In addition to the vulnerability of seedlings to predators, exposure to physical elements, especially extremes of temperature, may limit recruitment of some species to areas beneath other plant canopies (Shreve 1931). Midsummer temperatures of exposed soil surfaces in the Sonoran Desert can exceed 70°C, but shaded areas beneath trees and shrubs are markedly cooler (Shreve 1931; Jordan and Nobel 1979; McGinnies 1981). Experiments with the sahuaro, *Carnegiea gigantea* (see Turner et al. 1966), and *Agave deserti* (see Jordan and Nobel 1979) show complete mortality of seedlings exposed to the high temperatures of open microhabitats, even when water was abundant. Turner et al. (1966) demonstrated that field-transplanted *Carnegiea* seedlings provided with partial shade had considerably higher levels of survival. Seedlings of succulents are probably extremely susceptible to high temperatures because they store most of their tissue water directly above the soil surface and at the same time are unable to use transpirational cooling during the day because of their crassulacean-acid-metabolism (CAM) photosynthetic pathway. As a group, young cacti exhibit stronger associations with other perennials than do woody shrubs such as *L. tridentata* (table 7). These stronger associations may be a consequence of physiological limitations imposed by the CAM photosynthetic pathway that confront succulents but not woody perennials. Young individuals of some woody perennials can apparently

tolerate the physical extremes of open microhabitats and can persist in the open if they escape herbivory (pers. obs. of caged *Cercidium microphyllum* seedlings). However, a young succulent that germinates in an exposed location cannot escape the lethal extremes of the physical environment.

An exception to this pattern is seen in the distribution of young individuals of some *Opuntia* that reproduce vegetatively, including *O. fulgida*. Young individuals of *O. fulgida* are more commonly found in open areas away from the canopies of other plants (table 7). This species propagates principally by means of large, spine-covered sections of the stems that detach from the parent plant and take root on the soil surface. The relatively large size of these vegetative propagules, coupled with their dense coverings of light-colored, reflective spines, may afford protection from temperature stress, water stress, and herbivory. Cactus species that reproduce exclusively by means of small seeds all show very strong positive associations with canopies of other perennials in bajada habitats (table 7; McAuliffe 1984b).

In addition to protection from heat stress, the areas beneath other plant canopies can provide protection from damaging frosts. This may be an important factor in limiting the microdistributions of some succulent species in the northern and eastern parts of the Sonoran Desert (Steenbergh and Lowe 1977, 1983; Nobel 1980).

Various other factors may contribute to enhanced survival of seedlings located beneath other plant canopies. Soil nutrient levels beneath plant canopies may be increased by the accumulation of fine, windblown organic debris or by nitrogen fixation (Turner et al. 1966; Kershaw 1973; Tiedemann and Klemmedson 1973; Charley and West 1975; Barth and Klemmedson 1978; Lajtha and Schlesinger 1986). Accumulation of organic debris may also serve as a source for inoculating seedling root systems with symbiotic mycorrhizae that assist the young plant in obtaining water and nutrients (Sheps 1973; Bloss 1985).

Mechanisms Leading to Recruitment Away from Established Plants

Competition.—In some cases, competitive interactions may contribute to the dynamics of these systems by inhibiting the recruitment of new individuals near established plants. The complete absence of young *Larrea* plants and the rarity of young *Ambrosia* plants beneath canopies of older *Larrea* shrubs at the Dateland and San Luis sites may result from such inhibition. Recruitment of *Ambrosia* is greater in disturbed areas from which all plants have been removed than in areas occupied by *Larrea* and *Ambrosia* adults, suggesting competitive interactions of the two species. Field experiments have repeatedly shown that *Larrea* seedlings transplanted beneath *Larrea* adults experience higher mortality than do seedlings located away from canopies of adults (Sheps 1973; Boyd and Brum 1983). The role of competition in inhibiting recruitment has also been demonstrated in other structurally similar desert systems. Friedman (1971) and Friedman and Orshan (1975) demonstrated decreased survival and growth of seedlings of the shrub *Artemisia herba-alba* positioned near established conspecifics and individuals of the larger shrub *Zygophyllum dumosum* in the Negev Desert of Israel.

Unique characteristics of *Ambrosia*.—Factors other than the limitations placed

on recruitment by competition may contribute to abundant recruitment of *Ambrosia dumosa* and *A. deltoidea* in open space. Compared with seed production and seedling establishment in most desert perennials, these two species are prodigious. Following exceptionally heavy September rains in 1976 that triggered germination in the Sonoran Desert of southern California, Zedler (1981) reported the density of *Larrea tridentata* seedlings (765/ha) to be approximately six times the density of mature *Larrea* shrubs (122/ha). The relative abundance of *A. dumosa* seedlings was disproportionately greater; estimated *Ambrosia* seedling density (34,900/ha) was over 45 times the density of mature *Ambrosia*. Seedling establishment by *A. deltoidea* is similar. Following heavy germination in 1978, Goldberg and Turner censused the abundance and location of *A. deltoidea* and *L. tridentata* seedlings in eight plots (10 × 10 m) on the grounds of the Tumamoc Hill Desert Laboratory in Tucson, Arizona. Although the density of *A. deltoidea* adults (60 individuals/800 m²) was similar to that of *L. tridentata* adults (41 individuals/800 m²), 1001 *A. deltoidea* seedlings but only 124 *L. tridentata* seedlings were tallied (data obtained from unpublished maps provided by Turner). If herbivores exert a strong influence on seedling survival, such abundant establishment may provide a means by which greater numbers of *Ambrosia* eventually persist in open microhabitats.

Causes of Mortality in Adult Plants

Competitive interactions.—Local replacement of one plant by another that established beneath its canopy is common in the simple *Ambrosia-Larrea* communities, as well as in species-rich systems. Competition from a later-arriving plant may accelerate the loss of an original nurse plant (McAuliffe 1984a). However, sequences of occupation of a particular spot could occur in the absence of competitive interactions. If two plant species with similar longevity sequentially occupy individual patches, the usual temporal pattern is loss of the first arrival followed by the sole occupation of the patch by the second species. Although competition is not necessary for these types of sequential occupations, an effect of competition is to shorten the period during which the two species simultaneously occupy a patch.

There is little evidence that intraspecific competition leads to mortality in *Larrea* adults. At Dateland, mortality in *Larrea* is not related to distance to the nearest adult conspecific. The mean distance between dead *Larrea* plants and the nearest conspecific, 405 cm (SD = 186 cm, $n = 14$), is indistinguishable from the mean distance between pairs of living nearest neighbors, 408 cm (SD = 161 cm, $n = 83$; $t = 0.23$, $P > 0.50$). This pattern indicates that the likelihood of mortality among *Larrea* adults does not increase as a function of decreasing distance to conspecifics. If competition from neighboring plants does increase mortality, this mortality probably occurs in the early stages of the plant, as discussed earlier.

Other sources of mortality.—Factors other than competition, including effects of pathogens, predators, and local disturbance, may contribute to mortality in adult plants. For example, whereas mortality in adult *Larrea* is apparently unrelated to proximity of the nearest living conspecific, at Dateland, dead *Larrea*

shrubs are commonly associated with subterranean burrowing by *Dipodomys deserti*. This large kangaroo rat digs extensive burrow systems at the base of large *Larrea*; the average area covered by a single burrow system is 25.8 m² (SD = 5.8 m², $n = 10$). An average of 4.0 active and 2.5 recently abandoned *D. deserti* burrow systems per hectare was recorded at the study site. Together, active and abandoned burrows cover approximately 1.7% of the soil surface. Despite the relatively small area covered, 9 of 10 dead *Larrea* plants surveyed were found within the centers of these burrow systems. Mortality may be caused by direct damage to plant roots or by increased evaporation of soil moisture brought about by the extensive tunneling. In some desert systems, the burrowing activity of rodents may produce small-scale disturbances that have the same functional effect as disturbances produced by badgers in grasslands (Platt 1975).

ARE THE DYNAMICS OF DESERT PLANT COMMUNITIES UNIQUE?

The dynamics of desert plant communities have long been considered different from the dynamics of plant communities in regions that are more mesic. This view apparently originated from several publications in the early part of this century in which Shreve downplayed the importance of succession in the Sonoran Desert of Arizona and California. He repeatedly claimed that the species, and even the individuals, that are colonizers of cleared areas remain as final components of the vegetation (Shreve 1925, 1929, 1942). Muller (1940) arrived at similar conclusions based on his study of shrub communities in the Chihuahuan Desert. However, more-recent work in desert-scrub systems has documented changes in species compositions over time as evidence that succession does occur in desert plant communities (Wells 1961; Vasek 1979/1980, 1983; Webb et al. 1987). Shreve's conclusions were apparently in reaction to contemporary Clementsian views of succession and Clements' attempts to classify different types of desert plant communities within his successional scheme (Clements 1916, 1928, 1934; Weaver and Clements 1938). Shreve's clear opposition to Clements' ideas about succession and climax vegetation types is seen in his last publication (Shreve 1951). Although Shreve repeatedly denied that succession as conceived by Clements was an ongoing process in desert plant communities, he recognized vegetation dynamics similar to the ones I have described in this paper. Shreve (1937) briefly described the vegetation of sand dunes in the Gran Desierto region of northwestern Sonora, Mexico. He observed that only after dunes are colonized by the grass *Hilaria rigida* and the small shrub *Franseria* (= *Ambrosia*) *dumosa* did colonization by other perennials such as *Covillea* (= *Larrea*) *tridentata* occur. Nowhere, though, did Shreve use the term "succession" to describe this kind of vegetational change.

In this paper, I have described the dynamics of a desert plant community with the same analytical tools that Horn (1975) used to model succession in an eastern deciduous forest system. Although we both have used Markov chains, a specific difference exists. In the forest system modeled by Horn (1975), two tree species, gray birch and big-toothed aspen, represent transient states because they occur only in the earliest stages of succession. Whereas other species (e.g., black gum,

white oak, tuliptree, red maple, and beech) may replace birch and aspen, the two early-successional species are incapable of replacing the later-successional species. Barring the effects of large-scale disturbance, birch and aspen disappear during the course of succession. If this system is pictured as a digraph model, later-successional species form a strongly connected, closed subset of the digraph; the early-successional species form transient states weakly connected to this closed subset. Once transitions are made from the transient states to the strongly connected subset, return to these transient states is not possible (for a treatment of digraph representations of Markov chains, see Roberts 1976).

The Dateland and San Luis plant communities differ from the above forest system because the rapidly colonizing shrub species *A. dumosa* remains part of the system throughout the history of the community. There are no clear early- and late-successional species separated by a change in the presence or absence of these species over time. Although changes in relative abundances occur that sometimes have been referred to as "succession," no change occurs in the presence/absence vector.

I think the term *succession* is not suitable for describing the dynamics of these systems because of its ambiguity. If, on the one hand, succession is defined as change in relative abundances of species, then at Dateland and San Luis within all spatial scales, succession would be occurring from the time of initial colonization of a disturbed area until the time when a stationary distribution of states is reached and maintained. Once this stationary distribution is attained, succession would no longer occur within large spatial scales. Yet, it would still be occurring within the small spatial scale of the size of areas occupied by individual plants.

If, on the other hand, succession is defined as change in the presence or absence of species as proposed by Zedler (1981), succession would never occur at large spatial scales as long as both species were present, despite subsequent great changes in relative abundances. However, at a smaller spatial scale (the area occupied by individual plants), sequential changes in the occupancy of an area would produce changes in the vector of species presences and absences. At this scale, succession would always be occurring.

Advances in the understanding of desert plant communities will probably not result from arguing whether or not succession actually occurs in these systems. Rather, advances will occur when researchers accurately identify the types of dynamics that do exist, as well as the mechanisms that are ultimately responsible for these dynamics. This may in fact have been recognized by Shreve, who stated: "Many of the problems of the desert are intrinsic, while others are common to the desert and to moister regions, but can be attacked in a more effective manner under the clear-cut extremes of the desert. Indeed, it is not always possible to delimit the problems of the arid lands from those of the semi-arid ones, and there is no great importance in doing so." (1934, p. 200.)

SUMMARY

Many simple plant communities in extremely arid regions of the Sonoran Desert consist essentially of two shrub species, *Ambrosia dumosa* and *Larrea tridentata*.

These species exhibit completely different recruitment patterns and rates of population turnover. In these communities, the majority of space is devoid of perennial plant cover, and *Ambrosia* readily colonize this open space. Recruitment of *Larrea* occurs less frequently and is largely limited to areas beneath the canopies of large, older *Ambrosia* individuals. The dynamics of these systems can be modeled as Markov chains. Probabilities of transitions among states (open space, space covered by *Ambrosia* canopies, and space covered by *Larrea* canopies) are computed from data on spatial and temporal patterns of recruitment and mortality. Although the stationary distributions of states predicted by a homogeneous Markov chain are similar to those observed in undisturbed vegetation at two sites, a nonhomogeneous chain more accurately describes vegetational change following disturbance.

The dynamics of species-rich plant communities in less xeric parts of the Sonoran Desert appear to be qualitatively similar. One shrub species in particular, *A. deltoidea*, is capable of colonizing open space, whereas for most other shrub, tree, and succulent species, recruitment is largely limited to areas beneath canopies of other plants, especially canopies of *A. deltoidea*. Although seemingly more complex, a digraph model showing the transitions among states possesses the same fundamental characteristics as does a digraph of the simple two-species system.

A diverse set of mechanisms underlie these dynamics and include, in part, factors that influence seed distributions, germination success, and patterns of post-germination mortality. Even in the simple two-species systems, it is likely that no individual mechanism such as competition can be singled out as the predominant determinant of dynamics and, hence, of the patterns of community structure.

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