DYNAMICS OF MOJAVE DESERT SHRUB ASSEMBLAGES IN THE PANAMINT MOUNTAINS, CALIFORNIA[1]

ROBERT H. WEBB, JOHN W. STEIGER, AND RAYMOND M. TURNER
*United States Geological Survey, 300 West Congress Street FB-44,
Tucson, Arizona 85701 USA*

Abstract. We studied shrub communities in the Panamint Mountains of the Mojave Desert to determine whether vegetational changes after disturbance can be characterized as "succession" according to modern successional theory. We found, on a variety of disturbed and undisturbed sites, that the rate of change was a function of the type and age of disturbance.

Recent debris-flow deposits were colonized by shrub assemblages of different species composition than those on the surrounding, older debris-flow deposits and other geomorphically stable surfaces. Colonization of human-disturbed sites was highly variable, but species compositions were different from the predisturbance species composition. In *Grayia–Lycium* assemblages, *Grayia spinosa* reasserted its dominance over colonizers relatively quickly. In *Coleogyne* assemblages, typically found on older geomorphic surfaces, species composition differences persisted considerably longer, depending on the severity of the initial disturbance. Extremely stable assemblages, dominated by *Coleogyne ramosissima,* occurred on the oldest, least disturbed surfaces. The variability of species composition among disturbed sites was greater than the variability among undisturbed and geomorphically stable sites, in accord with "convergent succession."

Models of desert succession should consider several factors: (1) colonization is dependent largely on the severity of disturbances and residual biotic components; (2) the time span for recovery may be longer than past periods of climatic and geomorphic stability; and (3) colonizing species may have considerable range in their life-history strategies.

Key words: Coleogyne ramosissima; convergent succession; desert shrubs; disturbance; ghost towns; Grayia spinosa; Lycium andersonii; Mojave Desert.

INTRODUCTION

Desert plant communities (sensu Daubenmire 1968) have long been recognized as sensitive to disturbance. The cliché "easily scarred, slowly healed" implies that the rate of revegetation of disturbed desert areas is slow compared with human life spans. The questions of the rate and course of revegetation have been addressed in several studies of plots disturbed up to 66 yr prior to measurement (Wells 1961, Vasek et al. 1975*a, b,* Webb and Wilshire 1979, Lathrop and Archbold 1980*a, b,* Vasek 1980, Prose and Metzger 1985, Carpenter et al. 1986). These studies found that revegetation requires longer than 66 yr, is dependent on the severity of disturbance, and does not necessarily follow a predictable model of species-composition change.

The stability of desert shrub communities has received little attention, possibly because of an erroneous perception of lack of change (West 1982). Goldberg and Turner (1986) studied permanent plots in the Sonoran Desert measured at irregular intervals over 72 yr and found large fluctuations in cover and density.

Despite these fluctuations (18–69% turnover), the relative contribution of species remained similar. Species were functionally grouped according to life-history traits of longevity, survivorship, size, recruitment, and age structure. The endpoints in this continuum of strategy were species with long life spans, high survivorship, large size, and age structures skewed toward older individuals; and species with short life spans, low survivorship, small size, and age structures skewed toward young individuals. Their study suggests a hierarchical life-history structure that may affect revegetation in Upland Sonoran Desert communities.

In another study, Beatley (1980) measured fluctuations in cover of perennial shrubs in the northern Mojave Desert. Large turnovers caused by recurring wet-dry cycles resulted in 14% death and a 20–30% recruitment (by either seedlings or vegetative propagation) rate over a 12-yr period. However, neither species composition nor the relative proportion of each species changed. Beatley concluded that fluctuations in the cover of desert shrub communities are closely correlated with climate but are low enough to allow continued stability.

The results of revegetation and stability studies have created a polarization of opinion on whether plant

succession occurs in deserts. Shreve (1942) denied any species composition change following disturbances and observed virtually no biotic control of substrates or revegetation processes. Recent studies (Vasek and Lund 1980, Vasek 1980, 1983, West 1982) have challenged Shreve's assertions based on perceived seral stages associated with soil chemical changes resulting from pedogenesis. Shreve's proponents (e.g., Lathrop and Rowlands 1983) cite the absence of soil formation in deserts as a weakness in desert succession models. Moreover, while colonizers of disturbed areas may have a different species composition from the undisturbed vegetation (Wells 1961), they usually have some low-level representation in the undisturbed assemblages (Beatley 1976), blurring the distinction among seral stages. MacMahon (1981) refers to the "conspicuousness" of succession as increasing with the predictability of rainfall, and his model, which spans North American biomes, affords a means of reconciling views of succession in humid vs. arid areas. But a concensus as to the applicability of succession theory to deserts has not been achieved. Part of the problem stems from lack of field data to evaluate either rates of recovery from disturbance or long-term dynamics of shrub assemblages.

The Panamint Mountains of California offer an ideal setting for the evaluation of dynamics of Mojave Desert shrub communities. Debris flows periodically disturb vegetation, forming a mosaic of geomorphic surfaces of different ages. Humans have also disturbed vegetation periodically over the last 79 yr, leaving sites with varying degrees of revegetation. In some cases, human disturbance has crossed different-aged geomorphic surfaces. The purpose of this paper is to investigate the successional dynamics for two shrub communities, and to relate the results to modern successional theory.

METHODS

Setting

The Panamint Mountains are a north-south trending range bordering the west side of Death Valley (Fig. 1 inset). Elevations range from −100 m on the Death Valley side and +320 m on the Panamint Valley side, to 3550 m on Telescope Peak. The sites used in this study lie in an upland area of low hills and alluvial valleys at elevations of 1530–1830 m. The bedrock geology consists of Cambrian and Precambrian calcareous sedimentary rocks intruded with Tertiary granite along the axis of the range (Hunt and Mabey 1966). The principal rocks in the study areas are the Tertiary granitic intrusions and Precambrian Noonday Dolomite and underlying Kingston Peak Formations.

Climate of this area is poorly documented. The only climatological station in the range, at Wildrose Canyon (1250 m), has a mean annual precipitation of 191 mm and mean January and July temperatures of 4° and
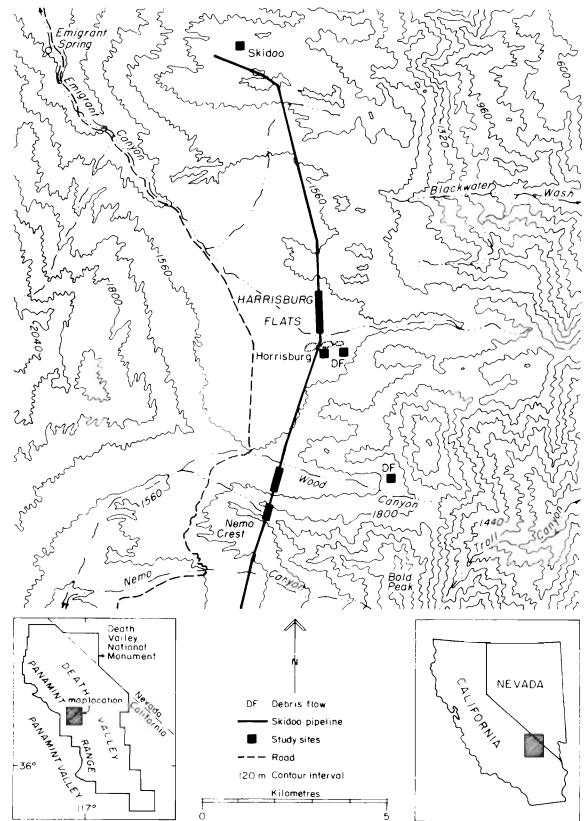

FIG. 1.   Location map for the Panamint Mountains study sites, California.

26°C, respectively, from a 10-yr record. From regional precipitation records, Hunt et al. (1966) estimated an annual precipitation range from 50 mm at the base to 380 mm at the top of the Panamint Mountains. The study areas reported here probably have an annual precipitation of 200–250 mm, most of which falls in winter months.

Vegetation assemblages

We studied the two upper elevation Mojave Desert community types of Grayia–Lycium and Coleogyne (Beatley 1976) lying between 1530 and 1830 m elevation. The presence/absence of Coleogyne ramosissima, with a variable lower elevation limit of 1580–1700 m, is the distinguishing floristic feature between these two communities, because both Grayia spinosa and Lycium andersonii occur in Coleogyne assemblages. Grayia–Lycium communities have not been reported in either the Black or the Grapevine Mountains on the east side of Death Valley (Kurzius 1981, Schramm 1982), but occur in the Cottonwood Mountains, the northerly extension of the Panamint Range (Peterson 1984). Coleogyne does not occur in the Grapevine Mountains (Kurzius 1981) but forms extensive stands in the Black Mountains (Schramm 1982) and in the Cottonwood Mountains (Peterson 1984).

Vegetation measurements

Vegetation measurements were made on debris-flow surfaces in Wood Canyon, in the ghost towns of Skidoo and Harrisburg and adjacent undisturbed sites, and along selected segments of the abandoned Skidoo pipeline (Fig. 1). Choice of these sites provided a comparison of colonization on naturally disturbed surfaces with revegetation of townsites, and both can be compared with the natural fluctuations in undisturbed *Grayia–Lycium* and *Coleogyne* communities. Study sites were chosen according to continuity of soils and geomorphic surfaces, visual uniformity in vegetation, spatial and temporal uniformity in disturbances, and the availability of nearby, representative undisturbed sites with the same environmental characteristics.

Perennial species were measured during May–June 1981 (May 1985 at Harrisburg) in transects established at each site. Only data pertaining to shrubs and sub-shrubs are presented here; grass species contributed between 1 and 3% cover in the sites. The low cover of grasses may be due, in part, to grazing by feral burros. Nomenclature follows Munz (1974).

Density of plants was measured using 50 × 2 m belt transects; transect width was increased to 3 m in low-density assemblages on debris flows. Cover of plants was measured using 50-m line intercepts on the margins of the belt transects. Transects were placed nonrandomly to obtain the most representative sample of vegetation at each site. The usual sample size was 400 m² of belt transects and 400 m of line intercepts unless otherwise noted in the tables of plant data. On two pipeline segments (Nemo Crest and Harrisburg Flat), the area of disturbance was not wide enough for belt transects, and only cover was measured using continuous line intercepts. Cover data was analyzed using principal components analysis (PCA; Gauch 1982).

Errors in measurement of density and cover were estimated to determine the reproducibility of transect data. The largest source of error in density measurements was the definition of an "individual"; certain vegetatively reproducing species (e.g., *Ephedra nevadensis*) develop clonal clumps and it is difficult to determine the degree of independence of individual stems. For this study, an "individual" was a plant that had <50% overlap in canopy with neighbors of the same species. Density measurements for nonclonal species were accurate to ±50 individuals/ha, and cover measurements were accurate to ±0.1%. Density data were not analyzed by PCA because densities of some cloning species (e.g., *Ephedra*) could not be measured reliably.

Scenes depicted in 22 historical photographs, taken between 1906 and 1960, were rephotographed as closely as possible to obtain additional life-history information. Repeat photography has been used extensively in evaluations of vegetation change (Rogers et al. 1984), especially in the Sonoran Desert region (Hastings and Turner 1965) and the central Great Basin (Rogers 1982).

We used repeat photographs to help determine sites for vegetation measurement, and to qualitatively assess the relative longevity and population turnover of species.

RESULTS: DYNAMICS OF *COLEOGYNE* COMMUNITIES

Debris flows in Wood Canyon

Wood Canyon (Fig. 1) has a surficial geology composed of modern and ancient debris flows on alluvial fans. Debris flows are water-based slurries of poorly sorted clay- to boulder-size material (Costa 1985) commonly occurring in desert areas. Debris flows are discrete events occurring rapidly during high-intensity or long-duration rainstorms, and consist of a source area (usually a steep chute), a leveed channel with net transport of debris, and an area of deposition. Debris flows have a characteristic poorly sorted, unstratified nature in their deposition area that is easily recognized.

Coleogyne assemblages of varying species composition mantle the ancient debris flows in eastern Wood Canyon. Wood Canyon has a mosaic of vegetation patches with distinct species composition corresponding with discrete debris-flow depositional areas of different geologic age. In other words, debris-flow depositional areas created at different times in the past support unique species compositions of *Coleogyne* assemblages.

Three debris-flow depositional areas were examined to determine the relative geologic age and species composition of perennial shrubs. Soils were described to determine a chronosequence of debris-flow events. Pedogenesis, the degree to which a soil has formed, is a complex function of climate, biological processes, slope, parent material, and time (Birkeland 1974). For eastern Wood Canyon, all of these factors except time can be held constant among debris flows. The local climate is similar for all three debris-flow depositional areas, which have a westerly exposure at elevations ranging from 1750 to 1830 m. *Coleogyne* assemblages surround all three areas, and the slopes (8–10°) are all similar. The parent material in the source area is granite. Therefore, differences in soil development among the three debris flows can be explained by time (geologic age) alone.

The soils developed on the debris flows indicate substantial differences in geologic age. For example, a recent debris-flow deposition area in eastern Wood Canyon, created during a large storm in February 1976 (P. Sanchez, *personal communication*), had a thickness of 1.5–2.0 m of unweathered cobbly, gravelly, loamy sand with no pedogenic alteration. This debris flow (A) was deposited over an older debris-flow deposition area (B). The older flow (B) had a thickness >65 cm, with weathered cobbles on its surface and a pedogenic calcic horizon consisting of calcium carbonate illuvially deposited on gravel and cobble faces. An old debris flow (C),

TABLE 1. Cover (*C*, %) and density (*D*, plants/ha) of selected shrubs on three debris-flow accumulation areas in Wood Canyon.

| | Debris flow* | | | | | |
| | A (youngest) | | B | | C (oldest) | |
Species	C	D	C	D	C	D
Coleogyne ramosissima	0.2	T†	17.6	12 500	20.6	14 500
Ephedra nevadensis	0.0	0	7.8	3100	5.5	8300
Chrysothamnus teretifolius	0.0	0	0.0	0	1.0	700
Lycium andersonii	0.3	100	3.1	1300	0.4	300
Thamnosma montana	0.0	0	T	200	0.3	100
Grayia spinosa	0.2	300	0.8	400	T	100
Artemisia tridentata	0.1	100	0.1	100	T	100
Eriogonum fasciculatum	0.3	100	0.1	300	T	200
Chrysothamnus nauseosus	T	300	0.0	0	T	100
Acamptopappus shockleyi	T	100	0.6	200	0.0	0
Haplopappus laricifolius	0.0	0	T	100	0.0	0
Gutierrezia microcephala	0.1	200	0.0	0	0.0	0
Lupinus excubitus	2.3	100	0.0	0	0.0	0
Total	3.5	1300	30.1	18 200	27.8	24 400

* Flow A occurred in 1976, B is of intermediate age (probably several thousand years), and C is the oldest debris flow (probably tens of thousands of years).

† T indicates the species was encountered in the transects with density <100 plants/ha or cover <0.1%.

1 km south of flows A and B but in a similar setting, had an illuvial clay horizon and a calcic horizon plugged with calcium carbonate.

The main distinction among these soils is the degree of carbonate accumulation in the soil profile. Carbonate accumulation is a valuable relative age-dating tool in desert soils (Machette 1985), although absolute dating is at best uncertain. Based on the degree of carbonate in the soils, debris flow B was much younger than debris flow C. The morphologies of the carbonate horizons suggested that several millennia separated debris flows A, B, and C in geologic age (see Machette 1985).

The three debris flows supported distinct shrub assemblages (Table 1). The youngest debris flow A was dominated in cover by *Lupinus excubitus*, a perennial species not found on the other two depositional areas. Obvious clumping of individuals made density measurements difficult; however, a census of species growing on debris flow A revealed 12 species not found on the adjacent debris flow B. Most of these species normally occurred on the steep source area, although some (especially *Atriplex canescens*) dominated on Harrisburg Flat 4 km away. Most of the colonizing plants were seedlings.

Debris flow B, of intermediate geologic age, supported an assemblage dominated by *Coleogyne*, with large contributions from *Ephedra nevadensis* and *Lycium* (Table 1). Although *Grayia* contributed <1% cover in the transects, *Grayia* locally dominated on debris flow B surfaces that have been slightly eroded.

Debris flow C, the oldest, supported an assemblage dominated by *Coleogyne* and *Ephedra* (Table 1). *Coleogyne* locally formed a nearly monospecific stand averaging 17% greater cover than on debris flow B.

Ephedra occurred in large clumps of apparently clonal origin. Thirteen shrub species were recorded on debris flow C, 21 on flow A, and 11 on flow B.

The debris flows in eastern Wood Canyon indicated that species composition differences in *Coleogyne* assemblages can be attributed to the age of the substrate. The only physical differences among the debris-flow depositional areas were those resulting from differences in geologic ages of the deposits. A direct comparison of the assemblages on debris flows A and B implied that, with increasing time, the unusual assemblage on debris flow A will be replaced with an assemblage dominated by *Coleogyne*. The amount of time required for this replacement is conjectural but may be on the order of millennia.

The Skidoo pipeline in Wood Canyon

An abandoned pipeline corridor (Fig. 2) crosses Wood Canyon about 3 km west of the debris flows (Fig. 1). This water pipeline, which traversed 35 km of the Panamint Mountains, was constructed in 1907 and was removed from Wood Canyon in 1917 (Greene 1981). The 3 m wide pipeline corridor consists of an abandoned road next to a pipeline trench, and the severity of disturbance, as indicated by the condition of the pipeline trench, decreased up slope. The pipeline crosses three distinct debris-flow depositional areas, labelled D, E, and F, with increasing elevation (Fig. 2). The elevation difference between D and F, the highest and lowest, is 60 m. The soils developed on the debris flows indicated only two distinct ages. Debris flow E, between flows D and F, had a calcic horizon with calcium carbonate occurring on the sides and bottoms of gravel and cobbles. Debris flows D and F had virtually identical soils with calcic and argillic (illuvial clay) hori-

FIG. 2. Photograph of the Skidoo pipeline corridor, looking due north through western Wood Canyon from Nemo Crest (photo by R. H. Webb 1981). The paler, nearly vertical stripe to the left of the letters is the pipeline corridor. Debris flows D, E, and F are labelled. Debris flows A, B, and C are not shown.
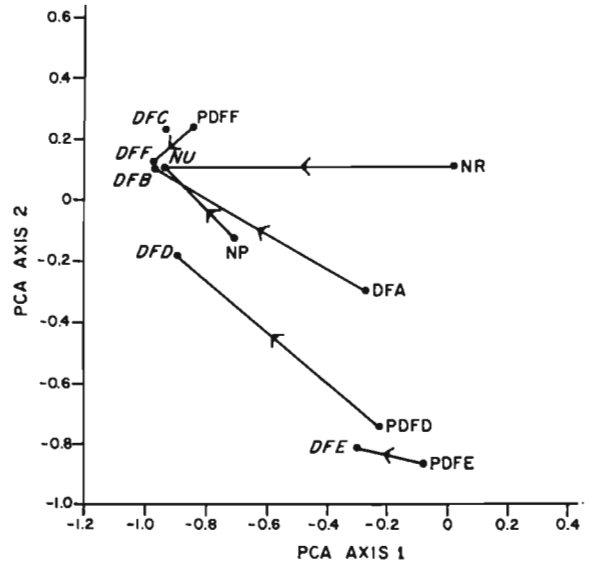

FIG. 3. Principal components analysis (PCA) ordination of cover data from *Coleogyne* communities in the Panamint Mountains. Paired disturbed/undisturbed sites are linked with arrows pointing toward the undisturbed site. Sites are Wood Canyon: DFA-DFF (debris flows A–F), PDFD-PDFF (pipeline corridors across debris flows D–F); and Nemo Crest: NP (pipeline corridor), NR (abandoned road), and NU (undisturbed hillslope).

zons; the calcic horizon had calcium carbonate fully coating gravel and cobbles. The parent materials, similar for the debris flows, are from the metasedimentary rocks of the Kingston Peak Formation, mostly dolomites and conglomerates. As before, absolute ages could

TABLE 2. Cover (*C*, %) and density (*D*, plants/ha) of shrubs on three segments of the Skidoo pipeline in Wood Canyon. Undist. indicates the control.

	Debris flow*							
	D				E (younger)			
	Pipeline		Undist.		Pipeline		Undist.	
Species	C	D	C	D	C	D	C	D
Coleogyne ramosissima	1.3	1500	8.2	4700	1.0	900	2.2	1330
Ephedra nevadensis	2.6	900	5.7	1500	2.9	700	1.1	600
Lycium andersonii	2.9	700	7.3	2600	1.9	1200	6.1	2000
Tetradymia axillaris	1.1	200	0.7	200	1.1	500	0.6	300
Grayia spinosa	0.1	400	3.2	1900	1.0	900	7.6	5100
Artemisia spinescens	T†	500	0.5	2100	0.0	0	0.2	300
Hymenoclea salsola	0.5	900	T	100	0.3	200	0.0	0
Acamptopappus shockleyi	4.5	7700	0.8	700	16.6	16 300	7.8	8500
Haplopappus laricifolius	2.2	3000	1.0	1500	T	100	0.1	100
Artemisia tridentata	0.0	0	0.0	0	0.3	100	0.0	0
Dalea fremontii	0.2	100	0.3	T	0.0	0	0.0	0
Chrysothamnus viscidiflorus	4.2	5000	T	100	0.1	100	0.1	T
Chrysothamnus nauseosus	0.1	100	0.0	0	0.1	100	0.0	0
Chrysothamnus teretifolius	0.0	0	0.0	0	0.0	0	0.0	0
Eurotia lanata	T	200	T	100	0.1	300	0.3	800
Total	19.7	21 200	27.7	15 600	25.4	21 400	26.1	19 000

* Debris flow E is younger than both flows D and F, and all are thousands of years old.
† T indicates the species was encountered in the transects with density <100 plants/ha or cover <0.1%.

not be estimated, but debris flow E was younger than debris flows D and F.

The vegetation assemblages out of the pipeline corridor on these debris flows (Table 2) reflected a pattern similar to that found in eastern Wood Canyon. Debris flow E supported an assemblage dominated by *Acamptopappus shockleyi*, *Grayia*, and *Lycium*. The assemblages on flows D and F were dominated by *Coleogyne*, with *Lycium* and *Ephedra* of secondary importance. Because of similarities in parent material and other environmental factors, the assemblage on flow E would be expected to change to a *Coleogyne*-dominated assemblage with time.

The pipeline corridor had been substantially revegetated (Table 2, Fig. 2). Total cover was slightly lower and total density was slightly higher in the pipeline corridor compared with the undisturbed debris flows after 64 yr. Species composition differences were large for flows D and E, however. The corridor on flow D had been revegetated with an assemblage dominated by *Acamptopappus* and *Chrysothamnus viscidiflorus*. The pipeline corridor on flow E was dominated by *Acamptopappus*, with twice the cover and density found in the undisturbed assemblages. The pipeline corridor on debris flow F, apparently the least disturbed of the three segments, had a cover of *Coleogyne* similar to the undisturbed assemblage. However, *Haplopappus laricifolius*, *Chrysothamnus nauseosus*, *C. viscidiflorus*, *C. teretifolius*, and *Acamptopappus* had a much larger cover in the pipeline corridor than in the undisturbed assemblage.

The debris flows in western Wood Canyon affirmed the findings in eastern Wood Canyon in several ways. *Coleogyne* dominated on older undisturbed surfaces.

TABLE 2. Continued.

	Debris flow		
	F		
Pipeline		Undist.	
C	D	C	D
12.0	11 700	13.6	7900
1.0	700	6.6	2000
0.2	300	2.3	1400
0.2	200	2.0	400
0.3	100	1.6	1000
0.1	1000	0.4	1900
0.8	1000	0.3	200
1.1	1100	0.2	100
3.2	3200	T	100
0.4	100	T	100
0.2	100	T	100
0.6	500	0.0	0
2.0	600	0.0	0
0.9	1100	0.0	0
0.0	0	0.0	0
23.0	22 200	27.0	15 200

TABLE 3. Cover (%) of shrubs in the Skidoo pipeline corridor at Nemo Crest. Data are from 250 m of transects, and are based on line intercept measurements.

Species	Undisturbed control	Pipeline	Abandoned road
Coleogyne ramosissima	11.7	1.6	0.6
Grayia spinosa	4.1	1.5	0.0
Lycium andersonii	3.0	1.2	0.0
Ephedra nevadensis	2.7	0.9	0.2
Eurotia lanata	1.0	0.8	0.6
Artemisia tridentata	0.5	0.7	1.9
Artemisia spinescens	0.1	0.3	0.0
Eriogonum fasciculatum	0.1	0.0	0.0
Chrysothamnus viscidiflorus	0.0	1.2	1.8
Chrysothamnus nauseosus	0.0	0.3	1.1
Acamptopappus shockleyi	0.0	0.2	0.4
Hymenoclea salsola	0.0	0.2	0.0
Tetradymia spinosa	0.0	0.0	0.5
Atriplex canescens	0.0	0.0	0.1
Haplopappus laricifolius	0.0	0.0	0.1
Total	23.2	8.9	6.7

While younger undisturbed surfaces had *Coleogyne* individuals, other species (especially *Grayia*, *Lycium*, and *Acamptopappus*) dominated. Human disturbance initiated a colonization assemblage of variable species composition, but which consistently contains *Acamptopappus*, *Haplopappus*, and *Chrysothamnus* spp.

The Skidoo pipeline at Nemo Crest

South of Wood Canyon, the Skidoo pipeline crosses Nemo Crest at an elevation of 1830 m (Fig. 1), traversing a 10–15° west-facing slope. The pipeline at Nemo Crest was removed in 1938 (Greene 1981), allowing 43 yr of recovery. A parallel service road was abandoned at the same time. The substrate at Nemo Crest is weathered metasedimentary rocks from the Kingston Peak Formation. Soils were not described at this site because bedrock and alluvium do not weather at the same rates. However, a shallow soil exhibiting pedogenic calcium carbonate was developed on the hillslope, and the site had undergone little erosion.

The total cover of shrubs in the pipeline and road was about one-third the cover of the undisturbed hillslope (Table 3). The vegetation outside the pipeline corridor was dominated by *Coleogyne* with *Grayia*, *Lycium*, and *Ephedra* contributing significant cover (Table 3). The pipeline trench and road, however, were dominated by a mixture of species, including *Artemisia tridentata*, *Coleogyne*, *Lycium*, *Grayia*, *Chrysothamnus viscidiflorus*, and *C. nauseosus*. Of the 15 shrub species encountered in the pipeline corridor transects, only 8 occurred in the adjacent undisturbed hillslope transect.

Principal components analysis of Coleogyne communities

To summarize the data from the *Coleogyne* communities, the cover data (Tables 1, 2, and 3) were ana-
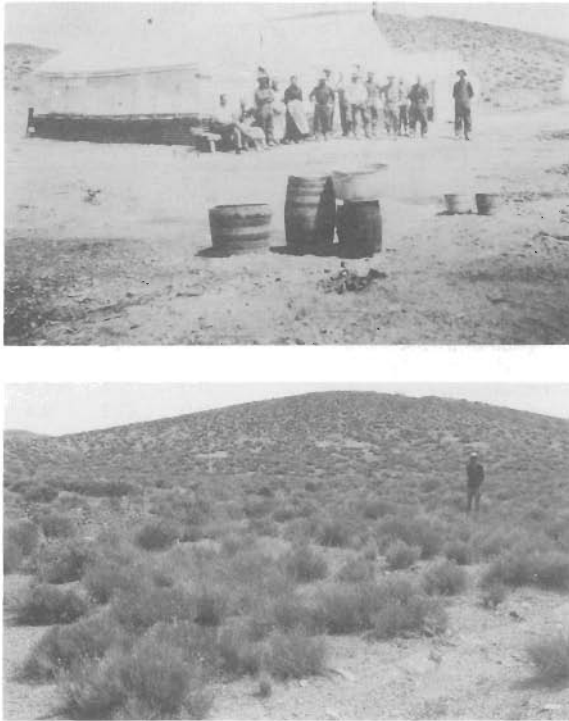
FIG. 4. Photographs of Harrisburg townsite, Panamint Mountains. (A) In May 1908 (courtesy of Death Valley National Monument). (B) In May 1984 (Raymond M. Turner collection, Stake #1120). Foreground shrubs are mainly *Chrysothamnus viscidiflorus.*

lyzed using principal components analysis (PCA; Fig. 3). Principal axis 1, which explains 49% of the total variance, clearly represents a disturbance gradient. The addition of principal axis 2 explains 68% of the vari-

ance; this axis partially reflects the effect of increasing elevation. Assemblages in pipeline corridors and on young debris flows plot to the right of assemblages on undisturbed sites or older debris flows. The tight clustering of undisturbed sites and older debris flows reflects the increasing dominance of *Coleogyne* at the expense of other species. The wide scatter of disturbed sites reflects the high variability in the composition of colonizing species on recently disturbed or geologically young sites.

RESULTS: DYNAMICS OF *GRAYIA–LYCIUM* COMMUNITIES

Harrisburg townsite

Harrisburg townsite (Fig. 1) was built in 1905 in response to gold mining on a low hill on the edge of Harrisburg Flats. At its peak in 1905, Harrisburg had a population of 100–300 miners with their tent houses spread around the north and south sides of this hill (Greene 1981). The population declined to about 20 miners by 1913. Old housesites were still apparent around the low hill, allowing measurement of recovery in a *Grayia–Lycium* community. In addition, another debris-flow deposition area created in 1976 borders the townsite, allowing a direct comparison of revegetation following natural and human disturbances.

An isolated section of Harrisburg townsite was located using aerial photography and an historical photograph (Fig. 4A). By 1908, this portion of the townsite was only slightly used, and was abandoned no later than 1910. Therefore, the section of Harrisburg measured represents 75 yr of recovery. Soil compaction resulting from the occupation had been completely ameliorated (Webb et al. 1986).

TABLE 4. Cover (*C*, %) and density (*D*, plants/ha) of shrubs at Harrisburg townsite and vicinity.

Species	1976 flow		Harrisburg townsite		Undisturbed control	
	C	D	C	D	C	D
Grayia spinosa	0.0	0	1.5	1800	9.7	5400
Lycium andersonii	0.4	100	0.7	400	7.2	3600
Ephedra nevadensis	0.0	0	9.8	4100	4.0	2500
Acamptopappus shockleyi	0.0	0	T*	100	1.4	4200
Chrysothamnus viscidiflorus	0.2	100	8.3	11 300	0.5	1900
Eurotia lanata	0.0	0	0.3	200	0.5	1700
Artemisia spinescens	0.0	0	T	100	0.3	1100
Haplopappus laricifolius	0.0	0	0.6	600	0.3	600
Tetradymia axillaris	0.0	0	0.0	0	0.2	200
Hymenoclea salsola	0.9	800	1.4	2300	0.2	400
Atriplex canescens	0.5	100	0.1	100	0.0	0
Salazaria mexicana	1.6	700	0.0	0	0.0	0
Thamnosma montana	1.4	400	0.0	0	0.0	0
Penstemon floridus	0.6	100	0.0	0	0.0	0
Chrysothamnus nauseosus	0.4	100	0.0	0	0.0	0
Encelia frutescens	0.3	1600	0.0	0	0.0	0
Artemisia rothrockii	0.1	100	0.0	0	0.0	0
Dalea fremontii	0.1	100	0.0	0	0.0	0
Total	6.5	4200	22.7	21 000	24.3	21 600

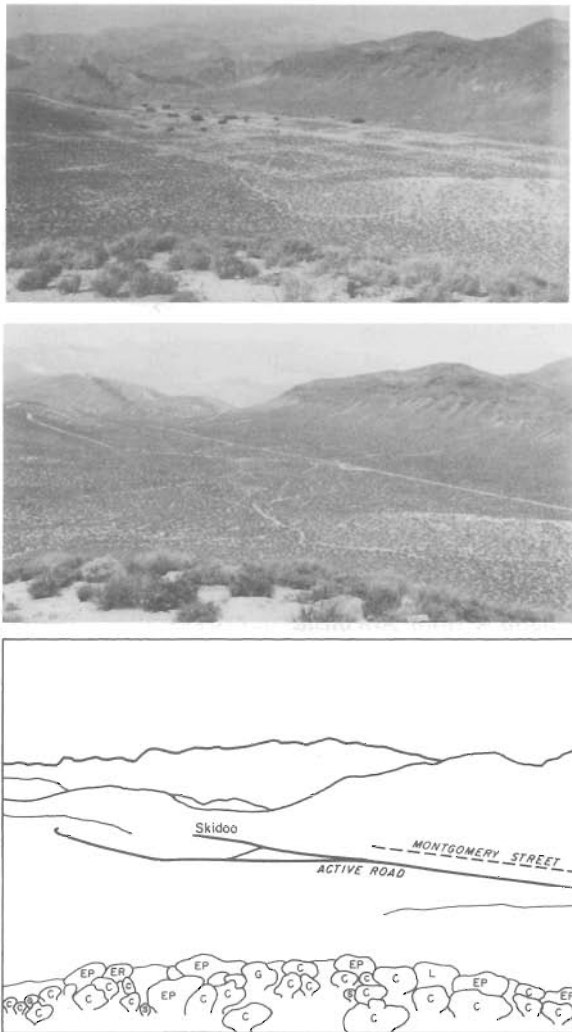* T indicates the species was encountered in the transects with density <100 plants/ha or cover <0.1%.

blage on the 1976 debris flow had little in common with the assemblages in the townsite or undisturbed area (Table 4). *Salazaria mexicana* and *Thamnosma montana* dominated an assemblage composed of 25 shrub species on the entire debris flow, compared with 10 species in the townsite and 9 species in the undisturbed area. Neither *Thamnosma* nor *Salazaria* occurred in the undisturbed assemblage, and both were restricted to rocky areas adjacent to debris flow levees and margins of depositional areas. Many other species on the debris flow, including *Penstemon floridus* and *Encelia frutescens*, normally occur in the source area.

The Skidoo pipeline on Harrisburg Flat

North of Harrisburg, the Skidoo pipeline corridor crosses Harrisburg Flat and climbs a low rocky slope (Fig. 1). This segment of pipeline was removed in 1917 (Greene 1981), leaving a 2–3 m wide corridor representing 64 yr of recovery. In addition, Harrisburg Flats is periodically inundated by floods (including the runoff from the February 1976 event), and the rocky slope has been severely eroded.

The undisturbed vegetation on Harrisburg Flats was dominated by *Grayia* and *Chrysothamnus viscidiflorus* (Table 5). The 1976 flood left fine-grained sediments plastered around the bases of shrubs on Harrisburg Flats. The adjacent pipeline corridor, with similar recent deposition of sediments, had an assemblage also dominated by *C. viscidiflorus* and *Grayia*. The two species had 60% more and 45% less cover, respectively, in the pipeline corridor than in the undisturbed area, and total cover was similar (Table 5). On the rocky slope, the vegetation assemblage in the undisturbed site was dominated by *Ephedra, C. viscidiflorus, Lycium,*

FIG. 5. Photographs of Skidoo townsite, Panamint Mountains. (A) In 1916 (Dane Coolidge photograph #309, courtesy of the Arizona Historical Foundation, Hayden Library, Arizona State University). (B) In May 1985 (R. M. Turner collection, Stake #1083). (C) Overlay showing silhouettes of perennials common to both photographs. C, *Coleogyne ramosissima*; EP, *Ephedra nevadensis*; G, *Grayia spinosa*; L, *Lycium andersonii*; S, *Stipa speciosa*; and ER, *Eriogonum heermanii*.

The vegetation in the abandoned townsite was compared with an undisturbed assemblage on the same geomorphic surface in a contiguous area. This surface, of probable debris-flow origin, had a soil with an argillic horizon and a plugged calcium carbonate horizon, indicating extreme but unknown antiquity (Machette 1985). The undisturbed vegetation and the assemblage in the townsite had similar total cover and density after 75 yr (Table 4). However, the undisturbed vegetation was dominated by *Grayia, Lycium,* and *Ephedra,* while the vegetation in the townsite was dominated by *Ephedra* and *Chrysothamnus viscidiflorus.* The assem-

TABLE 5. Percent cover of shrubs along two segments of the Skidoo pipeline at Harrisburg Flats. On the rocky slope, 445 m of transects were used, while 665 m were used on Harrisburg Flats. Data are from line intercept measurements. Pipeline and undisturbed (Undist.) transects were the same length and parallel, with a separation of 10 m.

Species	Rocky slope		Harrisburg Flats	
	Pipe-line	Un-dist.	Pipe-line	Un-dist.
Grayia spinosa	0.2	1.8	4.8	8.8
Chrysothamnus viscidiflorus	3.3	6.1	12.1	7.6
Lycium andersonii	0.9	4.9	0.6	2.2
Ephedra nevadensis	3.6	7.0	2.4	1.8
Artemisia spinescens	0.0	0.0	1.4	1.2
Atriplex canescens	0.0	0.0	1.4	0.3
Eurotia lanata		0.0	0.0	0.3
Tetradymia spinosa	0.2	0.8	0.5	0.2
Hymenoclea salsola	1.9	0.6	0.1	0.1
Haplopappus laricifolius	7.6	4.5	0.0	0.0
Dalea fremontii	0.7	0.2	0.7	0.0
Acamptopappus shockleyi	1.1	2.5	0.1	0.0
Salazaria mexicana	0.0	0.6	0.0	0.0
Total	19.5	29.0	24.1	22.5

TABLE 6.   Cover (*C*, %) and density (*D*, plants/ha) of shrubs at Skidoo townsite. MONT = Montgomery Street, MONTC = Montgomery control, SKID = Skidoo townsite, SKIDC = Skidoo control.

Species	MONT		MONTC		SKID		SKIDC	
	C	*D*	*C*	*D*	*C*	*D*	*C*	*D*
Grayia spinosa	9.8	5900	14.6	7400	5.5	5500	14.0	5000
Artemisia spinescens	10.1	28 400	4.8	12 400	2.1	7700	1.6	6400
Ephedra nevadensis	4.1	1500	3.2	800	3.3	700	7.2	2100
Lycium andersonii	1.1	1200	0.8	900	0.3	400	1.2	1100
Chrysothamnus viscidiflorus	0.5	700	0.2	200	4.2	2900	0.6	300
Hymenoclea salsola	0.1	T*	0.1	T	0.6	900	0.1	300
Eurotia lanata	T	100	0.0	0	0.2	100	0.0	0
Atriplex canescens	0.0	0	0.0	0	0.6	100	0.0	0
Artemisia tridentata	0.0	0	0.0	0	0.0	0	0.2	100
Chrysothamnus nauseosus	0.0	0	0.0	0	0.1	100	0.0	0
Acamptopappus shockleyi	0.0	0	0.0	0	0.0	0	T	100
Tetradymia spinosa	0.0	0	T	100	0.0	0	0.0	0
Total	25.7	37 800	23.7	21 800	16.9	18 300	24.9	15 400

* T indicates the species was encountered in the transects with density <100 plants/ha or cover <0.1%.

and *Haplopappus* (Table 5). The pipeline corridor had a vegetation assemblage of nearly one-third less cover, dominated by *Haplopappus, Ephedra,* and *C. viscidiflorus.*

On both the Harrisburg Flats and rocky slope segments of the Skidoo pipeline, the undisturbed and disturbed sites were essentially dominated by the same species, albeit with differing relative contributions of cover. This result may have derived from the continual natural erosional disturbance on both sites providing microsites for colonizing species.

Skidoo townsite

Skidoo (Fig. 1) was built in a long alluvial valley in 1906 in response to gold-mining operations in the surrounding hills (Greene 1981). The population of this large townsite peaked at 400–500 miners in 1907, but decreased to only a few miners in 1916 (Fig. 5) and was abandoned in 1917 (Greene 1981). Although a tourist attraction, Skidoo has remained largely undisturbed and represents a span of 64–74 yr of recovery. The low hills (Fig. 5) on the south are composed of granite and those on the north of the Noonday Dolomite. Alluvium at Skidoo is predominantly derived from granitic rocks and it has a poorly developed soil, manifested by thin calcium carbonate coatings on the bottoms of cobbles. This young soil apparently has developed on layers of water-laid sediment, suggesting a disturbance regime with a longer interval between disturbances than that occurring at Harrisburg Flat.

Two sites with different ages of recovery were established at Skidoo. Historical photographs suggest that Montgomery Street (at extreme right side of Fig. 5A) was cleared of vegetation and abandoned in 1907. Compaction measurements at Skidoo revealed residual compaction in the townsite (Webb et al. 1986) but not in Montgomery Street. This difference in residual compaction was hypothesized to represent a different stress regime facing colonizers, with the expected result of differences in species composition.

The vegetation in undisturbed controls for the two sites was similar (Table 6). The two had a similar total cover and were dominated by *Grayia* with varying contributions from *Artemisia spinescens* and *Ephedra.* Cover on the Montgomery Street site was similar to its adjacent undisturbed site, and both were dominated by *A. spinescens, Grayia,* and *Ephedra.* Cover at Skidoo townsite was 68% that of a nearby undisturbed site, but the only difference in the dominant species was the large cover of *C. viscidiflorus* (4.2%; Table 6). Residual compaction was apparently a factor in the reduced cover and slightly different composition of colonizers measured in Skidoo townsite.

Principal component analysis of Grayia–Lycium communities

Data on *Grayia–Lycium* communities, summarized by PCA (Fig. 6), reflect a scattered pattern for disturbed and undisturbed sites. The two axes explain 74% of the total variance, and a disturbance gradient occurs between the upper right and lower left of the ordination. Values for the three geomorphically stable sites (Skidoo control, Montgomery control, and Harrisburg undisturbed) are grouped closely together with the Montgomery Street site in the lower left corner of Fig. 6. However, values for the geomorphically unstable sites (rocky slope and Harrisburg Flat undisturbed areas) are grouped with the disturbed sites. The plant cover for most species on the Harrisburg debris flow is completely dissimilar to that of the other sites (compare Tables 4, 5, and 6). This ordination suggests that sites lacking disturbance, either natural or human-induced, are more similar than sites with similar disturbance histories.

PHOTOGRAPHIC EVIDENCE OF VEGETATION CHANGE

Comparison of plant data between disturbed and undisturbed sites requires some assumptions for meaningful ecological interpretation. Undisturbed assemblages may have changed significantly during the time

since abandonment of disturbed sites. Some constraint on disturbances is important to understand the effect of different biotic residuals (MacMahon 1980), in the form of individuals not destroyed or those arising from root–crown sprouting. To test these assumptions, scenes in 22 historical photographs from the Panamint Mountains were located as closely as possible and rephotographed. The time between the original and matched photographs ranged from 24 to 79 yr, and most of the sites measured were depicted in one or more photographs. A list of photographs used and one of life-history traits as observed in them are available on microfiche.[2]

Undisturbed vegetation assemblages had slightly increased in cover, and in some cases, they had increased also in density over the 79-yr period. The largest increases were observed in undisturbed *Grayia–Lycium* communities near Harrisburg and Skidoo townsites. The increase appeared to be due mainly to larger sizes of individuals and may have been related to the release from grazing pressure after abandonment of townsites and/or climatic effects (Beatley 1980, Goldberg and Turner 1986). Most of the changes illustrated by the photographs, however, were small enough to justify the assumption that undisturbed vegetation adjacent to disturbed sites is a good proxy for predisturbance conditions.

Disturbed areas had changed more rapidly than undisturbed areas. Pre-abandonment conditions usually consisted of bare, bladed, and compacted ground with widely scattered residual individuals (Fig. 4). Many of these residuals had survived and appeared much larger in the matched photographs. Changes in disturbed assemblages were overwhelming compared with changes in undisturbed assemblages when both appeared clearly in photographs (Fig. 5).

Identifiable individuals appeared in many photographs, providing some information on life-history traits for several important species. Many individuals appeared in the same location with approximately the same size after 69–78 yr (Fig. 5). In other photographs, principally at Skidoo townsite, recognizable individuals had increased dramatically in size and many individuals had been replaced. *Coleogyne* individuals changed the least in size of any species and few deaths or introductions were observed. Conversely, *Chrysothamnus viscidiflorus* and *C. nauseosus* individuals changed the most in size, and many new plants and loss of old individuals were observed.

DISCUSSION AND CONCLUSIONS

Disturbed and undisturbed shrub communities have changed at different rates during the last 78 yr in the
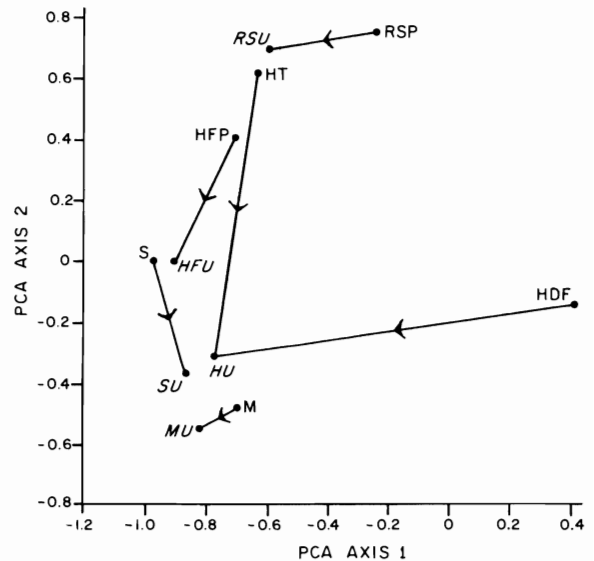
FIG. 6. Principal components analysis (PCA) ordination of cover data from *Grayia–Lycium* communities in the Panamint Mountains. Paired disturbed/undisturbed sites are linked with bars and arrows pointing toward the undisturbed site. Sites are Harrisburg: HDF (debris flow at Harrisburg), HT (Harrisburg townsite), and HU (Harrisburg undisturbed); Harrisburg Flats: HFP (Harrisburg Flats pipeline), HFU (Harrisburg Flats undisturbed), RSP (rocky slope pipeline), RSU (rocky slope undisturbed); and Skidoo: M (Montgomery Street), MC (Montgomery control), S (Skidoo townsite), and SC (Skidoo control).

Panamint Mountains. Sites disturbed and abandoned for 46–78 yr have been at least partially revegetated with colonizing shrub assemblages. Re-establishment of total shrub cover, one measure of recovery, generally requires 46–64 yr. Re-establishment of total shrub density is more variable, and in some disturbed sites, total shrub density can be significantly larger than the pre-disturbance density because of numerous small individuals of certain colonizing species. This pattern has been reported in other studies (Webb and Wilshire 1979, Carpenter et al. 1986).

In contrast, undisturbed vegetation has changed very little other than size increases of individuals during the same time period. Recruitment of new individuals was observed in photographs of undisturbed *Grayia–Lycium* communities, while *Coleogyne* communities were striking in their lack of change (Fig. 5). Clearly, the rate of change is a function of the disturbance history, and, to a lesser extent, the assemblage type.

After colonization, species compositions of disturbed sites converge toward the less-variable species composition of the undisturbed sites (Figs. 3 and 6). This convergence is in accord with observations and mathematical models of dynamics in forest ecosystems (Horn 1974, 1977). Such models require quantitative data on life-history traits such as establishment rates, mortality rates, and interspecific competition. Given
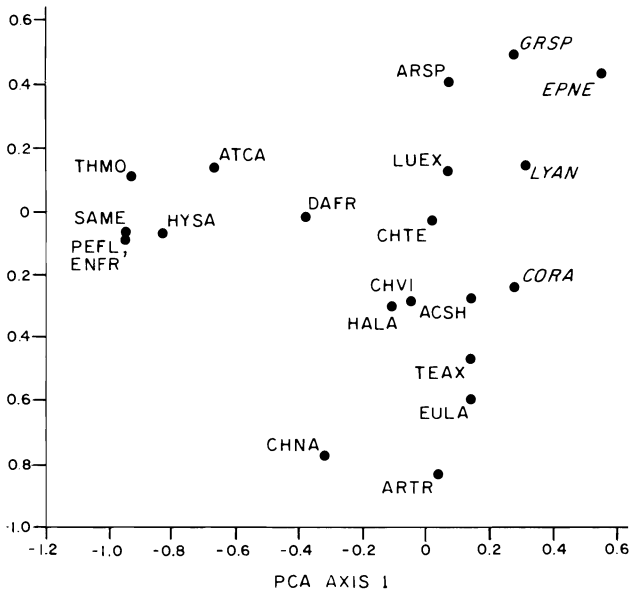
FIG. 7. Principal components analysis (PCA) ordination of cover data for all species measured in the Panamint Mountains. ACSH, *Acamptopappus shockleyi*; ARSP, *Artemisia spinescens*; ARTR, *Artemisia tridentata*; ATCA, *Atriplex canescens*; CHNA, *Chrysothamnus nauseosus*; CHTE, *Chrysothamnus teretifolius*; CHVI, *Chrysothamnus viscidiflorus*; CORA, *Coleogyne ramosissima*; DAFR, *Dalea fremontii*; ENFR, *Encelia frutescens*; EPNE, *Ephedra nevadensis*; EULA, *Eurotia lanata*; GRSP, *Grayia spinosa*; HALA, *Haplopappus laricifolius*; HYSA, *Hymenoclea salsola*; LUEX, *Lupinus excubitus*; LYAN, *Lycium andersonii*; PEFL, *Penstemon floridus*; SAME, *Salazaria mexicana*; TEAX, *Tetradymia axillaris*; THMO, *Thamnosma montana*.

quantitative data on these life-history traits, a Markov chain would be an appropriate model to describe the colonization and early turnover in species composition following disturbances in the Panamint Mountains. The scant data on life-history traits do not allow formulation of such a model, but the results presented here qualitatively support the concept of "convergent succession" (Horn 1977).

Convergence may never completely occur on older geomorphic surfaces. Rates of change are so slow that genetic changes may become important. A climatic change could completely alter the species composition on all surfaces regardless of age or disturbance. The different rates of change require any model of vegetation dynamics in the Panamint Mountains to account for a wide variety of biological and physical factors that vary in importance with increasing time after disturbance.

"Climax communities" are unlikely to exist and cannot be hypothesized for desert shrub assemblages in the Panamint Mountains because of climatic and/or species immigration instabilities. Desert shrub communities have been developing over the last 10 000 yr (Van Devender and Spaulding 1979), and the best paleoecological information suggests perhaps only 4000

yr of stability in modern shrub communities (Spaulding 1985). The ages of ancient debris flows are of the same order of magnitude, or are of far greater age, than this period of stability. The colonizers on the ancient debris flows probably were derived from surrounding pinyon–juniper assemblages, which mantled the Panamints until the Holocene (Wells and Woodcock 1985).

The differing rates of change discourage a simple model of vegetation dynamics. Assemblages are periodically disturbed in the normal course of alluvial processes in deserts. After a relatively rapid colonization and initial turnover in species composition, change occurs at an infinitesimal rate in terms of human life spans; short-term climatic fluctuations may be the only factor initiating change. Large ranges in the life-history traits of colonizers and the influence of residual biotic components can mask distinct seral stages. Long-term climatic changes are important because soil development, the apparent control on species composition in the vegetation mosaic, occurs on a time scale of millennia. The importance of geomorphic regimes and climatic fluctuations thus may be more important than intrinsic biological factors in controlling long-term vegetation dynamics.

Climatic factors and the importance of intra-assemblage species require a re-evaluation of the structure and stability of *Coleogyne* and *Grayia–Lycium* communities. The major floristic difference between the two communities is the presence/absence of *Coleogyne*. Both *Grayia* and *Lycium* have wide elevational ranges, while *Coleogyne* is usually restricted to upper bajadas (Beatley 1976). Given a documented downward movement in lower elevation limits for *Coleogyne* during the last 500 yr (Cole and Webb 1985), *Grayia–Lycium* assemblages could be considered as a "climatically induced disclimax" of what would normally be a *Coleogyne* community.

The dominant species in our desert assemblages appeared to follow an hierarchical order according to the type and severity of disturbance. A principal component analysis (PCA) ordination of all species at all sites (Fig. 7) explained 40% of the total variance with two axes. The dominants of old, undisturbed assemblages were grouped together at the far right of Fig. 7. Species grouped in the middle normally colonized human-disturbed sites or occurred on young debris flows. Finally, species grouped on the left most commonly occurred on the 1976 debris flows or on the youngest of the human-disturbed sites. While axis 1 represents a clear disturbance gradient, axis 2 weakly reflects elevation because *Grayia* and *Artemisia tridentata* are the extreme endpoints.

The life-history strategies of species may explain the array of species in Fig. 7. In desert plant communities, the dominants in undisturbed habitats are expected to be physiologically adapted to maintenance of long-lived individuals at the expense of reproduction (i.e., they are stress-tolerators: Grime 1979). Colonizers have the

reproduction-oriented traits of high seed production and aggressive establishment of short-lived individuals (stress-tolerant ruderals: Grime 1979). Few quantitative data are available for the life-history strategies of species in the Panamint Mountains, but the importance of some obvious characteristics is worthy of speculation for several species. We emphasize that interpretation of vegetation dynamics in terms of life-history strategies involves some circular reasoning in the absence of quantitative data on life-history traits, and that additional study is needed to test our conclusions.

Chrysothamnus viscidiflorus, the most widespread colonizing species among the disturbed sites, is known as an aggressive colonizer of disturbed sites in the Great Basin (Young and Evans 1974*b*). *C. viscidiflorus* produces flowers during summer months in all but the most severe-drought years, and produces abundant, small, wind-transported seeds (Young and Evans 1974*a*). Seedlings have a rapid growth rate and their development accelerates when competition from surrounding plants is removed (McKell and Chilcote 1957). *C. viscidiflorus* individuals remained in the same spot in matched photographs spanning only 25 yr or less. Other members of the genus *Chrysothamnus* have similar characteristics, albeit with interspecific variations (Young et al. 1984). *Chrysothamnus viscidiflorus*'s life-history strategy therefore emphasizes establishment and reproduction at the expense of longevity.

The autecology of *Coleogyne* is of critical importance to the vegetation dynamics. *Coleogyne* produces few, relatively large and immobile seeds, and has a low germination rate, with seedlings often arising from rodent caches (Bowns and West 1976, West 1983). *Coleogyne* seeds may germinate only after unusual early spring rains (Beatley 1974), suggesting that "pulse" climatic events are needed for establishment. *Coleogyne* has an extremely slow growth rate and long life span (Bowns and West 1976), and dominates on extremely stable landforms with maximum soil development (West 1983). *Coleogyne* individuals alter the soil chemistry around their bases (Bowns and West 1976). In historical photographs, *Coleogyne* individuals changed the least of any species and individuals appeared virtually identical in photographs spanning 78 yr (Fig. 5). *Coleogyne*'s life-history strategy therefore emphasizes maintenance of existing individuals, which only rarely become established.

Ephedra shares traits with species at both ends of the spectrum of life-history strategy. *Ephedra* is a long-lived evergreen species that produces large, relatively immobile seeds, like *Coleogyne*. However, *Ephedra* reproduces from both vegetative propagation and seed dispersal, and is a colonizer of many disturbed sites, as is *Chrysothamnus viscidiflorus*. Because of this range in life-history traits, *Ephedra* is suitable for revegetation of disturbed sites (Kay et al. 1977). *Ephedra* clearly possesses a life-history strategy suitable both for colonization and for maintenance of individuals. This

range in strategy would suggest that models of vegetation dynamics based on species categorized by rigid criteria (Grime 1979) are not appropriate for these desert shrub communities.

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