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Longevity, recruitment and mortality of desert plants in Grand Canyon, Arizona, USA

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Abstract. The demography of woody desert plants along the Colorado River in Grand Canyon, Arizona, USA, was analyzed using 355 pairs of replicated photographs taken as long ago as 1872. Longevity, recruitment, and mortality were determined for 38 species characteristic of ungrazed desert scrub. Individual plants that survived 100 yr or more included *Acacia greggii, Ambrosia dumosa, Atriplex canescens, A. confertifolia, Echinocactus polycephalus, Ephedra* spp., *Fouquieria splendens, Larrea tridentata, Lycium andersonii, Opuntia acanthocarpa, O. basilaris, O. erinacea, Pleuraphis rigida,* and *Yucca angustissima.* This is the first evidence of long lifespan for most of these species, particularly the succulents. Most of the long-lived species registered overall increases in population during the past century. Only four species with lifespans ≥ 100 yr had a net loss of individuals between 1889 and the present, and only two decreased between 1923 and the present. It seems likely that climatic fluctuations over the past century are largely responsible for these recruitment and mortality patterns; however, nurse plants, predation refuges and other biotic factors may also play a role.

Keywords: Demography; Desert shrub; *Ephedra*; *Larrea*; Lifespan; *Opuntia*; Repeat photography.

Nomenclature: Hickman (1993).

Introduction

Because few demographic studies in the warm deserts of the southwestern United States have spanned more than a decade or two (Goldberg & Turner 1986), demographic information for many long-lived species is incomplete or lacking. Certain general trends in perennial plant recruitment and mortality are well known, however. Because they depend upon highly variable climatic events, germination and emergence of the dominant woody plants are episodic (Shreve 1917; Barbour 1968; Sheps 1973; Beatley 1974; Ackerman 1979; Sherbrooke 1989; Bowers 1994). Recruitment into populations is rarer still and may require a series of favorable climatic events (Sheps 1973; Sherbrooke 1989; Parker 1993), escape from predation or competition (Steenbergh & Lowe 1977; McAuliffe 1988, 1990), various microhabitat factors (Shreve 1917; Turner et al. 1966; McAuliffe 1988), or a combination of these (Turner 1990). New plants may be recruited from persistent seed banks (e.g. *Cercidium microphyllum, Prosopis velutina, Encelia farinosa*) or from a transient seed pool (e.g. *Fouquieria splendens, Larrea tridentata, Carnegiea gigantea*) (Bowers 1994). Once a plant is established, its longevity partly determines the availability of safe sites for new recruits (Harper 1977; McAuliffe 1988). Adult mortality is brought about by a variety of events, including senescence (Martin & Turner 1977), drought (Jordan & Nobel 1982; Turner 1990), frost (Steenbergh & Lowe 1977; Turnage & Hinckley 1938; Bowers 1981; Webb & Bowers 1993a), fire (McLaughlin & Bowers 1982; Rogers 1985), competition (Vandermeer 1980), and livestock grazing (Niering et al. 1963; Webb & Bowers 1993b).

Not only do recruitment and mortality of a given species vary temporally in arid regions, they also vary spatially. For example, in MacDougal Crater, Sonora, Mexico, populations of *Larrea tridentata*, an evergreen shrub, declined 50 - 90 % during the first half of this century (Turner 1990), whereas during the same period on Tumamoc Hill, Tucson, Arizona, *L. tridentata* exhibited little mortality (Goldberg & Turner 1986). Observing different parts of the puzzle rather than the whole, some demographers have concluded that desert plant communities are remarkably stable (Shreve 1917), whereas others have stated that "desert communities are highly responsive to changes in the climatic regime under which they grow" (Turner 1990: p. 464).

Repeat photography offers a precise means of tracking individual desert plants over their lifetimes, which may range from a few years to a century or longer. In this paper, we report on recruitment, mortality, and longevity of the dominant desert plants along the Colorado River in Grand Canyon, Arizona. Our analysis was based on an archive of 1159 historical photographs from Grand Canyon. Of these, 357 show desert plants. The photographic record extends from 1872 to 1994; most of our information comes from photographs taken between

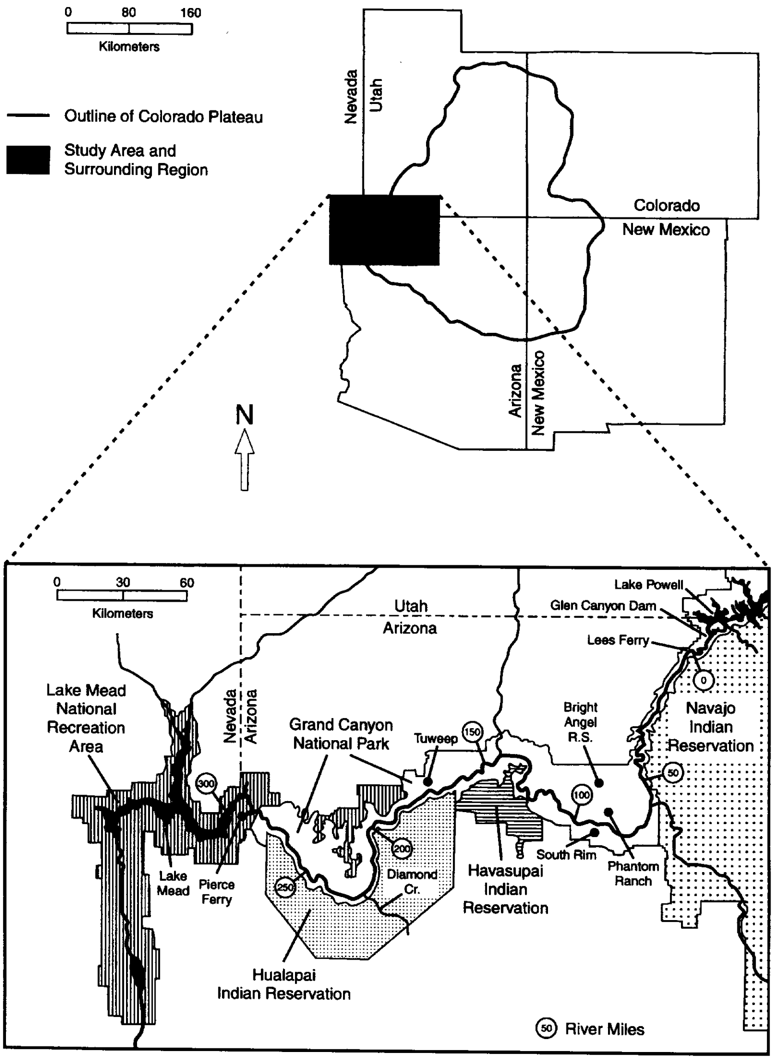

Fig. 1. Map of the Grand Canyon region showing locations and features mentioned in text.

1890 and 1993. Repeat photography has already been used in Grand Canyon to study vegetation change in the riparian zone (Turner & Karpiscak 1980), to analyze debris flows and rapids (Webb et al. 1989; Webb 1995), and to describe vegetation and geomorphic change along the river corridor (Stephens & Shoemaker 1987). Ours is not the first use of repeat photography in a demographic study (e.g. Turner 1990), but it is the first to undertake a quantitative demographic analysis of such a large number of replicated photographs.

Study area

Grand Canyon, Arizona, USA, lies between 35° 30' and 37° N, and between 111° 35' and 113° 30' W. The canyon is incised as much as 2000 m into the Colorado Plateau, a 336 700 km^2 region centered on the adjoining boundaries of Utah, New Mexico, Arizona, and Colorado (Fig. 1). We concentrated our efforts along the 446-km stretch of the Colorado River from Lees Ferry (mile 0, 950 m a.s.l.) to Lake Mead (mile 277, 366 m a.s.l.).

Substrates at river level are varied and depend on the source material. The most common rocks are sandstones, shales, and limestones of Cambrian to Permian age (Huntoon et al. 1986). Locally important rocks include Precambrian schist and granite and Quaternary basalt. The most common substrates in our replicated views are poorly sorted deposits of colluvial or debris-flow origin that range in slope from about 2 to 30°. Other landforms available for colonization by desert plants include aeolian dunes and landslide deposits, both relatively uncommon.

Four agencies – the U.S. National Park Service, the U.S. Bureau of Reclamation, and the Hualapai and Navajo nations – are involved with management or regulation of the river corridor and its resources in Grand Canyon (Fig. 1). The predominant anthropogenic impacts on desert vegetation have been artificial regulation of river levels, which allowed colonization of the former flood zone by desert plants (Turner & Karpiscak 1980; Carothers & Brown 1991; Webb 1995), and introduction of cattle and feral burros, which resulted in locally heavy grazing. Cliffs blocked the upstream and downstream movement of grazing animals, thereby restricting them to certain reaches (Ruffner 1977; Carothers et al. 1976; Stevens 1990; Webb & Bowers 1993b). The impacts of bighorn sheep and mule deer, the only large native herbivores, on desert-scrub vegetation have been minimal, especially compared to those of domestic livestock (Webb & Bowers 1993b).

Weather stations along the river corridor are Phantom Ranch, Lees Ferry, and Pierce Ferry (Table 1). Precipitation is biseasonal, with a warm-season peak from July through September and a cool-season peak from November through March. Winter storms originate as large-scale low-pressure frontal systems over the Pacific Ocean. Summer rains, characterized by thunderstorms that usually last several hours or less, result from advection of moist tropical air from the Gulf of Mexico or eastern North Pacific Ocean into Arizona. As a result of shading by vertical walls and cold-air drainage from high plateaus, winters at river level are cold, and daily minimum temperatures frequently drop below 0 °C in the coldest months, generally December and January. Summers are hot, and in June, July, and August, daily maximum temperatures of 40 °C or higher are common.

Desert-scrub vegetation occurs along the entire length of the Colorado River in Grand Canyon from near river level to an elevation of about 1130 m above the river (Warren et al. 1982). Species composition changes with increasing distance downstream from Lees Ferry (Warren et al. 1982; Phillips et al. 1987). Cold-desert plants typical of Great Basin desert scrub (*Atriplex confertifolia*, *Coleogyne ramosissima*, *Opuntia erinacea*, *Achnatherum hymenoides*) dominate colluvial slopes in the first 98 km. They gradually give way to a mixture of warm-desert species typical of the Mojave or Sonoran deserts, including *Ephedra* spp., *Fouquieria splendens*, *Encelia farinosa*, *Ferocactus cylindraceus*, *Larrea tridentata*, *Ambrosia dumosa*, and *Opuntia basilaris* (Phillips et al. 1987). Some of these (*E. farinosa*, *F. cylindraceus*) cannot tolerate temperatures colder than about – 7°C (Webb & Bowers 1993a). Slope aspect and substrate can be locally important in determining species composition (Warren et al. 1982) as can low temperature, which is in turn influenced by canyon width, aspect and elevation.

Table 1. Annual precipitation and temperature along the Colorado River in Grand Canyon, Arizona (data from Sellers et al. 1985).

Station	Elevation (m)	Precipitation (mm)	Average Daily Temperature Maximum (°C)	Average Daily Temperature Minimum (°C)
Phantom Ranch	783	230	27.5	13.9
Lees Ferry	978	150	24.6	8.9
Pierce Ferry	358	270	22.3	8.3

Methods

Repeat photography

Between 1985 and 1995, we acquired about 1 500 photographs from a number of archives with Grand Canyon holdings (Table 2) and from several individuals. These included 445 photographs taken by Franklin A. Nims and Robert B. Stanton in 1889-1890 and 198 photographs taken by Eugene C. LaRue during the U.S. Geological Survey Expedition in 1923. In addition, we used photographs and replicates taken by Raymond M. Turner between 1972 and 1984, and replicates made by Hal Stephens in 1968. Between 1989 and 1994, we replicated 1159 of the photographs in our collection. The Nims-Stanton photographs, taken at an average spacing of 1.8 km, provided unsurpassed coverage of desert vegetation. The LaRue photographs were not as systematic but still allowed us to assess the timing of demographic changes in some species. Photographs taken before 1890 or after 1923 were too few to allow determination of meaningful mortality and recruitment rates; still, they did provide additional information on longevity of some species. Altogether, 357 of our replicated views showed desert vegetation with sufficient clarity for interpretation and analysis. Of these, 346 were located on reaches that had never been grazed by domestic livestock (Webb & Bowers 1993b).

The amount and quality of scientific data that can be obtained from a pair of matched photographs depends on precise relocation of the original camera station. This is done by close inspection of the skyline and other landscape features in the original photographs (Rogers et al. 1984). To replicate the original views, we used two medium-format cameras (2-1/4 inch by 3-1/4 inch) and three large-format cameras (4 inch by 5 inch), together with a variety of lenses ranging in length from 47 to 135 mm. We used mostly black-and-white film and occasionally enhanced the appearance of cliffs or vegetation with yellow, orange, or red filters.

Table 2. Major historic photographers of desert vegetation along the Colorado River through Grand Canyon, 1872-1979, giving number of views used in our analysis.

Year	Archive or Expedition	Photographer(s)	Source	Number of views of desert vegetation
1872-73	Wheeler	Bell, O'Sullivan	NA, USGS	1
1872	Powell	Hillers, C. Powell	NA, USGS	3
1889-1890	Stanton	Nims, Stanton	NA, NYPL	268
1897-1920	James	James, Amsden, Maude	SM	10
1901	USGS	Carkhuff	USGS	1
1909	Stone	Cogswell	UCB, NYPL	2
1911	Kolb	Kolb	NAU	2
1923	USGS	LaRue, Freeman, Kolb	USGS	45
1934	Hatch	Fahrni	USHS	3
1937	Carnegie-Caltech	Campbell	Sharp	1
1938	Nevills	Clover	UU	1
1940	Nevills	Goldwater	CCP	1
1947-1959	Marston	Marston	HL	5
1949-1964	Reilly	Reilly	Reilly	2
1966	Butchart	Butchart	Butchart	1
1968	USGS	Stephens	Stephens	1
1973	PSU	Weeden	NPS	3
1974	MNA	Carothers, Karpiscak	USGS	1
1972-1976	USGS	Turner, Karpiscak	USGS	8
1982-1984	USGS	Turner	USGS	5
1960-1978	NPS	Euler	NPS	4

CCP	Center for Creative Photography	PSU	Pennsylvania State University
HL	Huntington Library	SM	Southwest Museum
MNA	Museum of Northern Arizona	UCB	University of California Berkeley
NA	National Archives	USGS	U. S. Geological Survey
NAU	Northern Arizona University	USHS	Utah State Historical Society
NPS	National Park Service	UU	University of Utah
NYPL	New York Public Library		

Photographic analysis

In the field, we analyzed each view by comparing the historical photograph with the present landscape. The substrate, most often talus containing prominent cobbles and boulders, remained remarkably stable during the interval between the original photograph and our match. Only a few rockfalls were recorded at our camera stations, mainly along the first 45 km of river corridor. Aeolian dunes, captured in several views, occasionally showed degradation or aggradation and were not used in our analysis. At several camera stations that are prominent scout points for major rapids, trampling by river runners had compacted soils or increased erosion. Otherwise, changes in substrate were minimal. Substrate control of the vegetation depicted in our photographs was subtle enough that we saw no need to stratify our results.

The resolution of the historical photographs varied considerably; in some, only foreground plants could be identified with any certainty. When comparing historical photographs with our matches, therefore, we interpreted only the area that was clearly visible in both views. Identifiable individuals present in the original photograph but missing from the present-day landscape were tallied as deaths. Those present today but not visible in the original photograph were counted as recruits. Only when an individual appeared to occupy the same spot, to be the same species, and to be of suitable size, did we count it as a survivor.

In the field, we used several criteria to determine which plants had survived, which were new, and which had died: (1) we compared the relative positions of individual plants and foreground rocks; (2) using a magnifier, we identified plants in the photograph on the basis of twig and leaf details; (3) we examined trunks and basal stems to verify the relative youth or age of plants. In some cases, we collected the oldest stems for radiocarbon dating. In the laboratory, we confirmed our field interpretations by comparing the original photograph with the printed match. It should be stressed that we interpreted the photographs, which entailed some degree of uncertainty. We rejected photographs that were blurred or that depicted unusual situations, particularly the burial or removal of most foreground rocks.

We tallied deaths and recruitments for each species,

Table 3. List of photographs showing the same individual plants in three or more views.

Species	Location	River Mile	Photographer (year)
Brickellia atractyloides	South Kaibab Trail	87.5	Leding (1952); Blaisdell & Wolfe (1963); Turner (1983, 1984); Webb (1994)
Ephedra nevadensis	Below Triple Alcoves	49.6	Hillers (1872); Turner (1972, 1983); Webb (1991)
	Cardenas Hilltop Ruin	71.5	Stanton (1890); Marston (1956); Brownold (1990)
	South Kaibab Trail	87.5	Leding (1952); Blaisedell & Wolfe (1963); Turner (1983, 1984); Webb (1994)
	Bedrock Rapid	130.5	Stanton (1890); Nevills (1938); Grua (1992)
	Lava Falls	179.3	Cogswell (1909); LaRue (1923); Grijalva (1994)
Galium stellatum	South Kaibab Trail	87.5	Leding (1952); Blaisedell & Wolfe (1963); Turner (1983, 1984); Webb (1994)
Larrea tridentata	Lava Falls	179.3	Stanton (1890); LaRue (1923); Campbell (1937); Turner (1990); Melis (1991)
Lycium andersonii	Below Triple Alcoves	49.6	Hillers (1872); Turner (1972, 1983); Webb (1991)
Opuntia erinacea	The Confluence	61.5	Hillers (1972); Turner (1972, 1982, 1983, 1984); Hymans (1993)
O. whipplei	Lava Falls	179.3	Cogswell (1909); LaRue (1923); Grijalva (1994)

then expressed the results as gains or losses divided by the total number of individuals. We calculated mortality rates using

$$M = [D/(D+S)] \cdot [n/100 \text{ yrs}] \cdot [100\%] \quad (1)$$

where M = mortality rate expressed as the fraction of deaths in percent of observed individuals per century, D = number of dead individuals, S = number of surviving individuals, and n = number of years between photographs. For recruitment, we used

$$R = [N/(N+S)] \cdot [n/100 \text{ yrs}] \cdot [100\%] \quad (2)$$

where R = recruitment rate expressed as the fraction of recruits in percent of observed individuals per century and N = number of new individuals. We tallied the number of individuals of each species that persisted from the time of the original photograph to the time of the match. We calculated percent change in population, ΔP, using

$$\Delta P = [(S+N)(100)/(D+S)] - 100. \quad (3)$$

Results

Quality of data

Using two cross-checking measures, we verified that our criteria for survival did indeed differentiate survivors from replacements (young plants of the same species in the same site). First, photographs of the same scene taken at different angles and in different decades show the same individuals in both the earlier and the later views. An example is a pair of photographs taken at Prospect Canyon. The 1909 view faces upstream, and the 1923 view looks downstream. The same individuals of *Ephedra nevadensis*, *Opuntia whipplei* and *L. tridentata* are present in the two photographs but are seen from different angles. The basal stems of these plants were relatively large for desert shrubs (>25 mm in diameter), and the position of the plants relative to nearby rocks had not changed, indicating that the plants were old individuals that had occupied the same site for many decades. Second, by matching photographs that were taken several decades apart at the same location, we were able to track individual plants from decade to decade (Fig. 2, Table 3). For example, a series of views from the South Kaibab Trail shows individual plants of *Brickellia atractyloides*, *Ephedra* sp., and *Galium stellatum* present in 1952, 1963, 1983, 1984, and 1994 (Table 3). A set of five views taken at various locations between 1972 and 1974 and matched in 1994 shows 11 of 14 *E. farinosa* surviving to the present day. Two more views taken in 1978 and replicated in 1994 show 10 of 17 *E. farinosa* plants surviving. We used the same criteria to evaluate the longevity of perennial grasses; because grasses cannot be dated using radiocarbon or xylem ring counts, however, we could not verify our longevity estimates.

For species capable of vegetative reproduction, we counted long-lived genets rather than short-lived ramets when evaluating longevity. The branches of *Yucca angustissima*, which may live as long as 50 yr, arise from a root crown capable of living at least 100 yr. We designated *Yucca* plants as persistent when they occupied the same spot (as determined from adjacent rocks or other stable features) over many years. Two cacti in our study area, *Opuntia basilaris* and *Opuntia erinacea*, produce short-lived joints from large underground crowns. When an aggregation of joints occupied the same spot in a pair of replicated views, we tallied it as a persistent plant. Joints of *Opuntia engelmannii* frequently take root where they touch the ground; the new plants produced in this manner are clones of the parent.

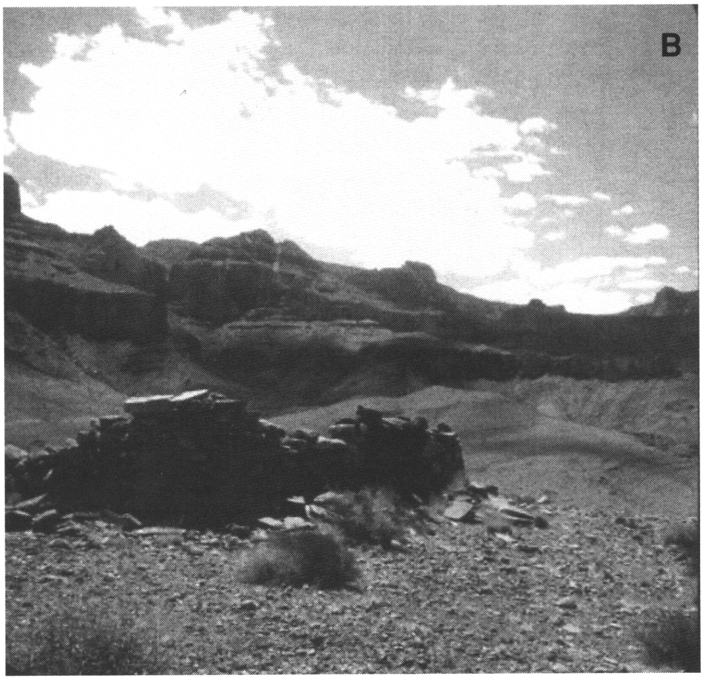

Fig. 2. At Cardenas Hilltop Ruin, mile 71.5, a time series of photographs showing survival of individual *Ephedra nevadensis* plants from 1890 to 1956, and from 1956 to 1990.
A. Photograph by Robert B. Stanton, Number 399, 1890, courtesy Still Picture Branch, National Archives.
B. Photograph by Otis (Dock) Marston, Number 566 GDCN 71.6, 1956, courtesy Henry E. Huntington Library.
C. (overleaf) Photograph by Tom Brownold, Stake 1439, January 25, 1990. Solid arrows show surviving *Ephedra* plants. Large open arrows show surviving *Lycium andersonii* plants. A plant of *L. andersonii* that survived from 1890 to 1956 and died before 1990 is shown by a small open arrow.

Although the ramets might not live long, the genet is capable of occupying the same site for 100 years, and we considered such plants to be persistent as well.

Plant demography

We were able to identify more than 60 species of perennials in the historical and modern views (Webb 1995). From the ungrazed reaches, we obtained at least some demographic information for 38 species, including one tree, 23 shrubs, 9 cacti and leaf succulents, and 5 perennial grasses. Using the plant checklist for Grand Canyon National Park (Phillips et al. 1987), we determined that these represent about 40 % of the woody, non riparian flora of the river corridor. We have selected for further analysis 18 species, grouped here as very long-lived (lifespan > 100 yr, mortality < 20 % per century); long-lived (lifespan > 70 yr, mortality > 20 % per century); moderate-lived (30 - 70 yr); and short-lived (< 30 yr). All are dominants in various desert scrub

assemblages along the river corridor. Table 4 includes additional species that are not dominants or that are represented in only a few photographs.

Very long-lived plants

Acacia greggii. This species is a shrub or small tree to 5 m tall. In desert scrub, 234 of 274 individuals survived from 1890 to the present, and 32 of 38 individuals survived from 1923 to the present (Table 4). The large number of persistent plants suggests that *A. greggii* should be long-lived (Goldberg & Turner 1986; Webb et al. 1987), and this is indeed the case. Our replicates of photographs originally taken in 1872 show 5 of 6 individuals that survived for 120 yr (Table 5). Tree-ring counts confirm that *A. greggii* can live at least 130 yr (Alex McCord, University of Arizona, Laboratory of Tree-Ring Research, pers. comm.).

Ephedra spp. Three species of *Ephedra* (*E. torreyana*, *E. nevadensis*, and *E. fasciculata*) are common along the river corridor from Lees Ferry to Lake Mead (Phillips et al. 1987). All three species are shrubs to 1 m tall. Because we encountered them most often in sterile condition, when they are difficult to distinguish, we combined them in our demographic analysis. Populations of *Ephedra* spp. have been very stable in Grand Canyon. Eight of 10 individuals survived from 1872 to the present. Of 800 individuals present in 1890, 664 survived to the present. Between 1923 and the present, 92 of 96 individuals survived (Table 4). The previous estimate of maximum lifespan, based on xylem ring counts of *E. viridis*, was 81 yr (Ferguson 1959). Ring counts show that *Ephedra* can reach an age of about 250 yr (Alex McCord, University of Arizona, Laboratory of Tree-Ring Research, pers. comm.).

Larrea tridentata. Populations of this 1.5-m tall shrub in Grand Canyon have been extremely stable over the past 70 yr (15 of 15 individuals survived) and over the past 100 yr (84 of 85 individuals survived) (Table 4). This stability is in accord with the great age reached by these plants, which is a function of their growth pattern. New stems arise not at the center of the crown but at the perimeter, eventually producing clonal rings (Vasek 1980). These rings can be long-lived; one estimate, an extrapolation based on radiocarbon dating of deadwood, puts maximum longevity of clonal rings at 11 700 yr (Vasek 1980). A more conservative estimate is 625 - 1250 yr (McAuliffe 1988). Using the method of Vasek (1980), a clonal ring near Lava Falls (mile 179.5) was estimated to be 2200 yr old (Theodore S. Melis, U.S. Geological Survey, pers. comm.).

Lycium andersonii. This species is a shrub to 2 m tall. Populations of *Lycium andersonii* in Grand Canyon have remained quite stable over the past century. Four of 4 individuals in photographs taken in 1872 persisted until the present day, showing that *L. andersonii* can live at least 120 yr (Table 5). The other matched photographs also suggest long life: 77 of 89 plants persisted from 1890 to 1990, and 6 of 6 plants survived from 1923 to 1993 (Table 4). The maximum observed lifespan of a close relative, *L. berlandieri*, is 72 yr (Goldberg & Turner 1986). The discrepancy in age is doubtless an artifact; the maximum observed longevity of their study species could not exceed the duration of their study, which was 72 yr.

Table 4. Long and moderate-lived plants identified in photographs taken by F. A. Nims and R. B. Stanton in 1889-1890 or by E. C. LaRue in 1923, Grand Canyon, Arizona. The matched photographs, which were taken 100-104 years later (for Nims-Stanton originals) or 67 - 70 yr later (for LaRue originals), showed at least one surviving individual of each species. All data are from desertscrub communities at ungrazed sites.

Species	1890-1990s Photograph pairs with persistent plants	Number of persistent plants	1923-1990s Photograph pairs with persistent plants	Number of persistent plants	Previous maximum longevity	Source
Achnatherum hymenoides	1	1	-	-	none	
Acacia greggii	95	234	14	32	72	Goldberg & Turner 1986
Agave utahensis	-	-	1	1	55	Nobel 1987
Ambrosia dumosa	5	13	-	-	36	McAuliffe 1988
Aristida purpurea var. *nealleyi*	5	4	-	-	none	
Atriplex canescens	2	2	-	-	29	Goldberg & Turner 1986
A. confertifolia	5	13	-	-	none	
Baccharis sergiloides	1	1	-	-	none	
Bernardia incana	1	5	-	-	none	
Brickellia atractyloides	3	5	-	-	none	
Cercis occidentalis	1	1	-	-	none	
Coleogyne ramosissima	1	2	-	-	400	Bowns & West 1976
Echinocactus polycephalus	1	1	-	-	none	
Echinocereus triglochidiatus	5	6	-	-	none	
Encelia farinosa	0	0	6	1	32	Goldberg & Turner 1986
Ephedra spp.[a]	162	664	21	77	81	Ferguson 1959
Fouquieria splendens	3	1	6	12	200	Darrow 1943
Galium stellatum	6	7	1	2	none	
Haplopappus salicinus	1	1	-	-	none	
Krameria erecta	1	3	-	-	none	
Larrea tridentata	17	84	3	15	11 700	Vasek 1980
					1250	McAuliffe 1988
Lycium andersonii	31	77	4	6	72[b]	Goldberg & Turner 1986
L. fremontii	1	1	-	-	72[b]	Goldberg & Turner 1986
Muhlenbergia porteri	2	c	-	-	none	
Opuntia acanthocarpa	3	4	-	-	none	
O. basilaris	13	25	4	3	none	
O. engelmannii	6	12	-	-	none	
O. erinacea	12	21	-	-	none	
O. whipplei	3	4	-	-	none	
Petrophyton caespitosum	1	3	-	-	none	
Peucephyllum schottii	4	2	2	4	none	
Pleuraphis rigida	15	43	3	3	> 100	Nobel 1981
Prosopis glandulosa	54	c	-	-	none	
Rhamnus betulaefolia	1	1	-	-	none	
Sporobolus flexuosis	4	5	-	-	none	
Trixis californica	1	1	-	-	none	
Yucca angustissima	3	15	-	-	none	
Ziziphus obtusifolia	2	2	-	-	none	

[a] = Includes *Ephedra nevadensis*, *E. fasciculata* and *E. torreyana*.
[b] = Based on *Lycium berlandieri*.
c = Individual plants not tallied.

Long-lived plants

Ambrosia dumosa. This species is a low shrub to 0. 5 m tall. The 1890 photographs depicted 23 individuals, of which 13 survived to the present (Table 4). It does not appear in any 1923 photographs from ungrazed sites. Estimates of lifespan have ranged from 36 yr (McAuliffe 1988) to 'extremely long-lived' (Muller 1953). McAuliffe calculated average rather than maximum longevity, which is one reason for the discrepancy between his estimate and ours. The discrepancy might also reflect a shorter lifespan in a more arid site. The moderately high mortality rate (43% per century) (Table 6) suggests that the plants do not live much longer than 100 yr. Ours is the first confirmation of long lifespan for this species.

Atriplex confertifolia. This 1-m tall shrub commonly reached 100 yr in age in our study. 13 of 19 individuals

Table 5. Long-lived plants identified in photographs taken by J. K. Hillers in 1872, Grand Canyon, Arizona. The matched photographs, which were taken 118-122 years later, showed at least one surviving individual of each species. All data are from desert scrub communities at ungrazed sites.

Species	Number of photograph pairs with persistent plants	Number of persistent plants	Previous maximum longevity (yrs)	Source
Acacia greggii	4	5	72	Goldberg & Turner 1986
Ephedra sp.	4	8	81	Ferguson 1959
Lycium andersonii	4	4	72[a]	Goldberg & Turner 1986
Opuntia erinacea[b]	2	3	none	

a = Based on *Lycium berlandieri*; b = Includes one *O. erinacea* hybrid.

survived from 1890 to the present (Table 4). The moderate rates of mortality and recruitment (32 % per century and 50% per century, respectively) (Table 6) suggest that *A. confertifolia* is adapted for relatively long life in stable communities.

Opuntia basilaris. *Opuntia basilaris* is a low, spreading cactus to 0.3 m tall. The individual joints are not long-lived, but the root crowns can apparently live a century or more. In the 1890 photographs, 25 of 34 individual crowns persisted from 1890 to the present (Table 4). In the 1923 photographs, 3 of 4 individual crowns survived until the present (Table 4). Mortality and recruitment per century was about the same in the 1923-1993 period as in the 1890-1990 period (Tables 6 and 5).

Opuntia erinacea. This is a low, spreading cactus that forms clones up to 2 m in diameter. The clones, which arise from a large root crown, can persist in the same spot for at least 120 yr. Three of four individuals in photographs taken in 1872 persisted until the present (Table 5). More common in our study were 100-yr old plants: 21 of 28 individuals in the 1890 photographs survived to the present (Table 4). No individuals were depicted in the 1923 photographs.

Pleuraphis rigida and other perennial grasses. Except for *Pleuraphis rigida*, which was represented by 43 persistent individuals, the number of persistent grass plants in our study was small (Table 4), largely because we restricted our tally to foreground plants that were clearly visible. Our replicated views suggest that five species of perennial caespitose grasses (*Aristida purpurea* var. *nealleyi*, *Muhlenbergia porteri*, *Achnatherum hymenoides*, *Pleuraphis rigida*, and *Sporobolus flexuosus*) might live 100 yr (Table 4). Most perennial grasses are believed to live less than 10 yr on average (Canfield 1957; Wright & Van Dyne 1976; West et al. 1979), but maximum lifespans of 29 to 43 yr have been reported for some (West et al. 1979), and *P. rigida* has been reported to live for "hundreds of years" (Nobel 1981).

43 of 63 *P. rigida* individuals in the 1890 photographs survived until the present day (Table 4). In Fig. 3, five persistent individuals can be readily discerned in the foreground. The 1923 photographs did not show any clearly visible *P. rigida*. Given the relatively low mortality rate of this species (32% per century) (Table 6), it seems likely that it can survive longer than a century. The mortality rates of *A. hymenoides* (50% per century) and *S. flexuosus* (67 % per century) are about the same as for some plants known to live 100 yr or more. We could not calculate mortality for *A. purpurea* or *M. porteri*; in the first case, no deaths were detected in our matched photographs, and in the second case, individual plants could not be distinguished.

Table 6. Mortality and recruitment of selected plants in matched photographs taken 100-104 years apart, Grand Canyon, Arizona. The originals were taken by F. A. Nims and R. B. Stanton in 1889-1890. Mortality and recruitment are reported as a percent of the total population per century (see text). All data are from desert scrub communities at ungrazed sites.

Species	% per century		% Change
	Mortality	Recruitment	
Acacia greggii	15	27	+17.2
Ambrosia dumosa	43	28	− 21.7
Atriplex canescens	89	92	+38.9
A. confertifolia	32	50	+36.8
Echinocactus polycephalus	80	97	+520.0
Echinocereus triglochidiatus	14	50	+71.4
Ephedra spp.	17	22	+6.8
Fouquieria splendens	75	50	− 50.0
Galium stellatum	0	22	+28.
Larrea tridentata	1	7	+5.9
Lycium andersonii	13	14	+1.1
Opuntia acanthocarpa	76	64	− 35.3
O. basilaris	26	50	+47.1
O. engelmannii	33	78	+200.0
O. erinacea	25	43	+32.1
Peucephyllum schottii	0	50	+100.0
Pleuraphis rigida	32	25	− 9.5
Yucca angustissima	55	58	+9.1

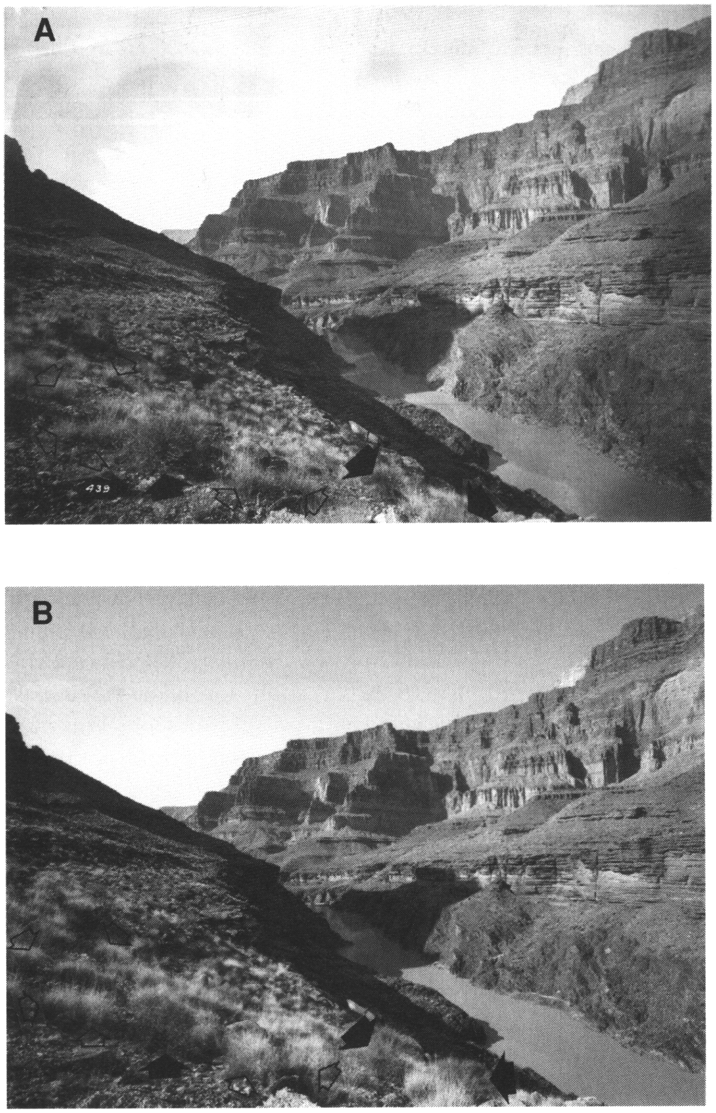

Fig. 3. At mile 128.4, a pair of photographs showing survival of *Ephedra nevadensis* and *Pleuraphis rigida* from 1890 to 1992. **A.** Photograph by Robert B. Stanton, Number 570, 1890, courtesy Still Picture Branch, National Archives. **B.** Photograph by Robert H. Webb, Stake 2580, February 23, 1992. Solid arrows show surviving *Ephedra* plants. Open arrows show several of the many surviving *P. rigida* plants.

Yucca angustissima. This species is a caulescent leaf-succulent shrub to 2 m tall. 15 of 33 individuals shown in the 1890 photographs survived to the present (Table 4) ; no plants were depicted in the 1923 photographs. As for the *Opuntia* spp. described above, the below-ground parts live a century or longer, whereas the stems, produced via offshoots from the base or from woody rhizomes, are shorter lived. Mortality and recruitment rates are similar (Table 6), indicating a population that has moderate turnover and a slight upward trend in total number of individuals.

Moderate-lived plants

Atriplex canescens. This is a shrub to 1.5 m tall. No individuals were depicted in the 1923 photographs; in the 1890 photographs, only two of 18 plants survived for 100 yr (Table 4). The high rates of recruitment (89% per century) and mortality (92% per century) (Table 6) suggest that most individuals do not live for a century. The life-history strategy also suggests that *A. canescens* is not adapted for long life: the plants typically colonize disturbed soils and may remain as a minor component of the community in later successional stages (Webb et al. 1987).

Echinocactus polycephalus. A clump-forming cactus to 0.6 m tall, *E. polycephalus* has several to many spherical or cylindrical stems. In our replicates of the 1890 photographs, only one of five plants survived to the present (Table 4). The survivor was a massive individual with 30 stems. The high rates of mortality and recruitment (Table 6) suggest that few plants live for 100 yr.

Encelia farinosa. Encelia farinosa is a shrub 0.5 to

Table 7. Mortality and recruitment of selected plants in matched photographs taken 67-70 years apart, Grand Canyon, Arizona. The originals were taken by E. C. LaRue in 1923. Mortality and recruitment are reported as a percent of the total population per century (see text). All data are from desert scrub communities at ungrazed sites.

Species	% per Century Mortality	Recruitment	% Change
Acacia greggii	13	4	−10.5
Agave utahensis	60	64	+71.4
Encelia farinosa	56	69	+840.0
Ephedra spp.	3	8	+9.4
Fouquieria splendens	35	28	− 16.7
Larrea tridentata	3	3	0.0
Opuntia basilaris	18	53	+200.0
O. whipplei	0	35	+100.0
Peucephyllum schottii	14	14	0.0

1 m tall. Before 1890, the distribution of *E. farinosa* in Grand Canyon may have been limited by cold temperatures (Webb & Bowers 1993a; Webb 1995). In our matched photographs from ungrazed reaches, no *E. farinosa* plants survived from 1890 to the present. One of five plants apparently survived from 1923 to the present (Table 4) ; two more individuals persisted on grazed sites. Although these plants may have been replacements rather than survivors, all three appeared old (as suggested by thick bases, many living stems, and a considerable proportion of dead stems), and we have treated them as persistent individuals. The high turnover in the population (Table 7) suggests that survival for 70 yr is not customary for *E. farinosa*. Our matches of three 1957 views show 18 of 49 individuals surviving to the present day, which suggests that a lifespan of 37 yr is not uncommon for this species in Grand Canyon. Maximum observed longevity near Tucson was 32 yr with few individuals surviving more than 7 yr (Goldberg & Turner 1986). The discrepancy between their estimate and ours may be a result of sample size. *Encelia farinosa* appeared in more than 100 of our matched photographs but in only 7 of their 9 permanent plots (Raymond M. Turner, pers. comm.), and we were therefore more likely to discover any very old plants that existed.

Ferocactus cylindraceus. This is a cylindrical cactus to 1.5 m tall. Of 264 individuals present in 1890 and 70 present in 1923, none survived until the 1990s. Five of 8 individuals in one photograph persisted from 1938 to the 1990s, suggesting a maximum longevity of about 55 yr. This is much shorter than a 90-yr estimate based on net CO_2 uptake and a water index (Nobel 1988). If the plants typically survived 90 yr in Grand Canyon, we would expect to see at least a few 70-yr old individuals persisting from the 1923 photographs to the 1990s photographs, yet we did not. Height-growth relationships over a two-year period for 68 plants at mile 179.4 indicate that a plant 90 cm tall is ca. 36 yr old and that a plant 120 cm tall (close to the maximum height) is ca. 45 yr old (Bowers unpubl. data). This is in accord with the maximum age indicated by repeat photography. *Ferocactus cylindraceus* populations increased dramatically in Grand Canyon after 1890 (Webb & Bowers 1993a). On average, 128% more *F. cylindraceus* individuals were visible in our matches than in the 1890 views.

Fouquieria splendens. This 4-m tall shrub had a high turnover in Grand Canyon. From 1890 to the present, mortality and recruitment per century were 75% and 50%, respectively (Table 6). From 1923 to the present, they were 35% and 28% (Table 7). Maximum observed lifespan of *F. splendens* is 72 yr (Goldberg & Turner 1986). Although maximum estimated lifespan is 150-200 yr (Darrow 1943), the high turnover in Grand Canyon suggests that this is an overestimate. Only one of four individuals in the 1890 photographs persisted to 1993, whereas 12 of 24 individuals in the 1923 photographs survived (Table 4). It is not unusual, then, for plants to live 70 yr, whereas it does seem unusual for them to live 100 yr. Darrow's (1943) estimated lifespan, which was based on stem tip growth over several years, most likely did not take into account unusually dry years, when growth is minimal.

Short-lived plants

Certain woody or suffrutescent plants common in desert scrub along the river corridor could be identified in many photographs but never survived as long as 70 yr. These included *Baccharis sarothroides*, *Dyssodia porophylloides*, *Eriogonum fasciculatum*, *Gutierrezia sarothrae*, *Machaeranthera pinnatifida*, *Pluchea sericea* and *Porophyllum gracile*. Of these, *E. fasiculatum*, *G. sarothrae* and *P. gracile* are known to be short-lived (Vasek et al. 1975; West et al. 1979; Goldberg & Turner 1986). The others share life-history traits that often accompany short lifespan, including high production of small, readily dispersible seeds; ability to colonize disturbed habitats; and high importance on young substrates and lessened importance on older substrates (Bowers & Webb unpubl. data).

Discussion

On ungrazed reaches, individuals of 38 perennial plant species persisted from 1890 or 1923 to the present. Of these, 22 were frequent enough in the photographs to yield reliable mortality and recruitment rates (Tables 5 and 6). The remainder were too infrequent to allow confident interpretation of trends. Most of the long-lived species registered overall increases in population during the past century (Tables 5 and 6). Only four species with lifespans ≥ 100 yr lost numbers between 1889 and the present (Table 6), and only two decreased between 1923 and the present (Table 7). Recruitment was not evenly spread across the decades between 1890 and the 1990s; comparison of Tables 5 and 6 shows that some species, especially *Acacia greggii*, *Larrea tridentata* and *Opuntia basilaris*, increased more between 1890 and 1923 than between 1923 and the 1990s.

Although little is known about longevity of desert plants (Goldberg & Turner 1986), the available literature suggests that the lifespans of woody plants in desert communities are comparable to those of more mesic environments. For example, *Pinus ponderosa*, a common forest tree of the southwestern United States, often lives to 115-165 yr of age and occasionally to 300 yr or older (Sudworth 1917) ; two Sonoran Desert dominants, *Cercidium microphyllum* and *Carnegiea gigantea*, have lifespans of about 400 yr and 150-200 yr, respectively (Shreve 1951). We confirmed long lifespans for several species, including *A. greggii*, *E. nevadensis*, and *L. tridentata*, and provided new evidence for long life in several others, namely *Ambrosia dumosa*, *Echinocactus polycephalus*, *Lycium andersonii*, *Opuntia basilaris*, *O. engelmannii*, *O. erinacea*, and *O. whipplei* (Tables 4 and 5). Repeat photography also enabled us to confirm moderate lifespan of certain species. *Agave utahensis* and *E. farinosa*, for instance, rarely survived for 70 yr and never survived for 100 (Table 4).

Some of our lifespan estimates conflict with earlier reports. With repeat photography, we were able to follow individuals for as long as 120 yr, longer than any previous study in the region. It is not surprising, therefore, that our longevity estimates for *Acacia greggii*, *Ambrosia dumosa*, *Atriplex canescens*, *Ephedra*, *Lycium andersonii* and others exceed previously published lifespans. Ring counts confirm that *A. greggii* and *Ephedra* sp. are indeed long-lived. Other discrepancies may be more surprising. We estimated a maximum age of 55 yr for *Ferocactus cylindraceus*, whereas Nobel (1988) calculated that the plants can reach at least 90 yr in age. Our empirical data suggest that his model does not work for mature plants in Grand Canyon. Our matched photographs suggested that *Encelia farinosa* can live 70 yr, more than twice as long as previous estimates. The individuals in question appeared old, and we have provisionally treated them as survivors.

Limited data from Grand Canyon suggest that grazing by domestic livestock greatly accelerates turnover of many woody plants and also shortens their lives (Webb & Bowers 1993b). In the absence of grazing, certain supposedly short-lived perennials seem to reach extremes of longevity, for instance, 70 yr for *Encelia farinosa* and 100 yr for *E. polycephalus*. Dominants such as *L. tridentata* and *Ephedra* spp. easily live 120 yr or longer. Long-lived species, by occupying recruitment sites for many years, can control establishment of new seedlings (Harper 1977). In Grand Canyon, the increase in number during the past century of most of the species listed in Tables 5 and 6 suggests that, despite their low mortality and long life, the dominant plants did not limit the availability of recruitment sites.

In the arid southwestern United States and northwestern Mexico, patterns in recruitment and mortality may vary considerably from place to place over the same period. Turner (1990) noted high turnover in populations of large woody plants in MacDougal Crater, Sonora, a site that has experienced no livestock grazing and little human disturbance. Of 103 *L. tridentata* present in 1907, 38 survived until 1986. 11 new plants became established in the 79-yr period. 14 of 54 long-lived leguminous trees (*Olneya tesota*, *Cercidium microphyllum* and *Prosopis* sp.) survived 79 yr, and 18 became established. Turner (1990) ascribed the high mortality in *Larrea tridentata* and *Cercidium microphyllum* to prolonged drought from 1936 to 1964. Pulses of establishment, particularly for *Carnegiea*, *Prosopis*, and *Encelia*, seemed related to unusually heavy rain during certain seasons. Overall, the gains and losses in plant numbers showed high responsiveness to climatic fluctuations (Turner 1990). During the same period, long-lived species such as *Carnegiea gigantea*, *Cercidium microphyllum*, and *Prosopis velutina* lost and gained numbers slowly at Tumamoc Hill, Tucson, Arizona. Only the smaller, shorter-lived species showed high turnover (Shreve 1929; Shreve & Hinckley 1937; Goldberg & Turner 1986). As at MacDougal Crater, high mortality was ascribed to regional drought, particularly from 1948 to 1957, and establishment followed unusually heavy precipitation events (Goldberg & Turner 1986). In Grand Canyon, patterns of recruitment and mortality more closely resembled those at Tumamoc Hill than those at MacDougal Crater in that populations of the very long-lived species remained relatively stable while many of the shorter-lived species underwent substantial fluctuations.

It seems likely that in Grand Canyon climatic fluctuations over the past century are largely responsible for the recruitment and mortality patterns that we documented. Climate is probably not the only factor involved; nurse plants, availability of recruitment sites, predation refuges, etc. likely play significant roles. Future research will focus on climatic change in Grand Canyon during the past century, especially with regard to recruitment and mortality of the dominant perennials, and on modeling the dynamics of the desert plant communities along the river corridor.

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