

Sonoran Desert Fire Ecology¹

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Abstract.--Repeated observations of permanent plots and transects are used to evaluate adaptive responses of individual species and communities of perennial plants following fires that occurred in 1974. Positive adaptations are common, but are weakly developed. Recovery is taking place, but at a very slow rate. Several decades, at least, will be required for full recovery.

INTRODUCTION

An important objective of fire-ecology research is determination of natural fire frequencies (Vogl 1977). In most vegetation, fires leave dateable evidence such as scars on tree rings (Ahlgren and Ahlgren 1960). In the Sonoran Desert, however, growth is not restricted to a single period, and growth rings are not always reliable indicators of age (e.g., Judd et al. 1971). An alternative approach to fire history determination using fire-related adaptations is explored in this report. Separate analyses of the interrelationship of climate, fine fuels, and survival, as well as individual species responses, are being prepared.

Plant species of some vegetation have been shown to have evolved characteristics that favor survival of fire (Gill 1977). In this paper we evaluate post-fire responses of perennial plants, measured for three to five years, to determine whether or not positive adaptations to fire are sufficiently common to suggest an evolutionary history of repeated burning.

Little is known of the ecological role of fire in the deserts of western North America. Most studies of desert fire have actually dealt with the semiarid fringe of the desert--the foot-hill shrubland and woodland of the Great Basin Desert (Wright et al. 1979), the desert grassland of the Southwest (Humphrey 1958), and upper altitude sites in the Chihuahuan Desert (Ahlstrand 1979). One reviewer (Humphrey 1974) regards desert fire to be uncommon, except in areas

dominated by native perennial grasses. Studies in the Mojave Desert (Beatley 1966) and the Great Basin Desert (Rogers 1980), however, indicate that sufficient fuel can be supplied by introduced annuals. Similar species of annuals are abundant at times in the Sonoran Desert (Franz 1977).

During recent years, fires have occurred throughout the Desert. Arizona Bureau of Land Management (BLM) records show that during the seven-year period 1973-1979, 210 fires burned 36,621 ha in the Arizona Upland and Lower Colorado subdivisions (Shreve 1951) of the Desert. Most fires occur in the Arizona Upland, and it is probable that local topographic and climatic conditions, as well as behavior patterns of prehistoric and modern peoples, could result in much higher frequencies at some locations than at others. The above figures suggest that fire could occur in cycles shorter than the life span of longer-lived Desert species (Shreve 1951), and could be a significant selective force in shaping the life-history traits of individual species.

METHODS

Following fires that occurred in 1974, permanent plots and transects were established in burned, and adjacent unburned, vegetation at two sites in south-central Arizona. One site (Dead Man Wash) is about 45 km north of Phoenix (SE $\frac{1}{4}$ sec. 27, T. 6 N., R. 2 E., Gila and Salt River Meridian), and consists of a 65 ha burn that began at the side of Interstate Highway 17, and was probably man-caused. The other site (Saguaro) is about 50 km east of Phoenix (T. 3 N., R. 8 E., Gila and Salt River Meridian), 105 ha in size, and was also man-caused. The fires occurred in May and June.

At each site, two to three chart quadrats (100 to 300 m²) were established on each of three exposures. Total plot area is 900 m² at Dead Man Wash, and 1500m² at Saguaro. To supplement plot information, six point-quarter transects (250 to 500 m) were located in predominantly burned vegetation at Dead Man Wash, and four burned

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(500 m) and four unburned (250 m) transects were established at Saguaro. Transects were sampled at 10 m intervals.

Percent kill (proportion of photosynthetic surface scorched or consumed by fire), percent consumption (reduction of total biomass), and resprouting (shoot or leaf growth from roots or scorched stems) were estimated and recorded for all perennial plants during the initial survey. Position of all plants in plots was recorded on graph paper. Identities of mostly consumed plants were determined by comparing remaining stem or root tissues with that of living plants. Errors in identification are most likely for rarer species, and do not greatly influence most results of the study, except the values for species richness and diversity. Presence and resprouting of living plants was recorded during resurveys after four years (51-58 months) at Dead Man Wash, and after three years (34-40 months) at Saguaro.

Data from both surveys are used for mostly qualitative judgements of species and community adaptations to fire (Gill 1977, Mutch 1970). The analysis is limited to perennial plant species, and to the following species traits: 1) bud protection and resprouting, 2) seedling establishment, 3) resistance to fire, and 4) flammability. Bud protection and resprouting are reviewed by Gill (1977). Seedling establishment may have been from seeds surviving fire in the soil, seeds remaining on burned plants, or seeds dispersed from resistant plants within the burn, or from unburned areas.

Resistance to fire, for the purposes of this study, is defined as survival without resprouting or seedling establishment. Survival might thus result from physical resistance to kill and consumption, might be a chance event due to occurrence of a skip (area of unburned vegetation within the larger area of the burn), or might be due to habitat characteristics that decrease fire probability through fuel reduction.

The last trait considered, flammability, is assumed to be closely related to consumption. Whether or not greater consumption is a consequence of greater flammability of one or another species in the way that Mutch (1970) found the litter of fire-prone vegetation to be more easily burned is uncertain. Other characteristics such as canopy height and shape, or interspecific relations with understory species, might also be important.

Community characteristics considered include plant density, species richness (number of species), species diversity (Brillouin index, Pielou 1975), and adaptive characteristics (Grime 1979) typical of early ecological succession.

SPECIES ADAPTATIONS

Resprouting, seedling establishment, and resistance were observed in 13 of 19 species

present in all burned plots (Tables 1 and 3). Resprouting was observed in 15 of the original species present in all plots and transects (Tables 1 and 3). Although frequent among the species present, resprouting replaced only seven percent of combined plot and transect numbers, and only two percent of the plants in all burned plots. Resprouting species were more common in Saguaro plots than in Dead Man Wash plots. Most resprouting was by woody shrubs, and least by cacti.

Seedling establishment was more abundant than resprouting, and resulted in replacement of 22% of the original plants in all burned plots. Most (82%) seedlings were *Ambrosia deltoidea*. Seedling establishment was greatest at Saguaro, partly because of colonization by two species not recorded during the original survey (*Cassia covesii* and an unidentified species of *Castilleja*), but also because of the greater success of *A. deltoidea* seedlings. At the time of the original survey, seedlings were abundant in the north-facing plots at Dead Man Wash, but few survived until the resurvey. Seedling establishment accounted for 52% of all plants present in burned plots at the time of the resurvey.

Resistance to burning occurred in 9 of the original 19 species in all burned plots. These plants represent 9% of the original number. Most (75%) of the survivors were either *A. deltoidea* or *Larrea tridentata*. Unburned skips were common at both sites, and *A. deltoidea* usually survived by being entirely skipped. In contrast, *L. tridentata* usually survived because of incomplete kill of stems and leaves.

Flammability varied from 95% (*A. deltoidea*, Table 3) to 1% (8 species, Tables 1 and 3). An attempt was made to identify correlation between flammability and survival, but scattergram plots of flammability and resprouting, and other forms of survival, showed no relationship. Most cactus species were only slightly consumed, but *A. deltoidea* was usually 100% consumed unless skipped.

COMMUNITY ADAPTATIONS

Total species densities declined in all burned plots, with greatest decline at Dead Man Wash (Table 2). Transect densities also declined at Dead Man Wash, but no change occurred on Saguaro transects. Resurvey density at Dead Man Wash ranged from 21% to 36% of pre-fire density. At Saguaro, post-fire density ranged from 70% to 100% of pre-fire. This was due both to skips, and to the reproductive success of *Encelia farinosa*, *A. deltoidea*, *C. covesii*, *Castilleja*, *Acacia constricta*, *Acacia gregii*, and *Lycium* spp. *A. deltoidea* decreased in burned plots at both sites, but increased on transects. *E. farinosa* made the greatest relative increase. Cactus species decreased at Saguaro, and on burned plots at Dead Man Wash. *E. farinosa* appears to qualify, at least in a relative sense, as a ruderal. Its increase while cactus species declined tends to

Table 1.—Dead Man Wash. Data include numbers of plants on both surveys (N1 and N2), numbers of plants resprouting (RS1 and RS2) on each survey, numbers of seedlings and resistant plants, and mean percent kill and consumption.

Species	Burned plots						Burned plots and transects					
	N1	N2	RS1	RS2	Seedlings	Resistant	N1	N2	RS1	RS2	%Kill	%Consump.
<i>Ambrosia deltoidea</i>	275	49	0	0	35	14	298	178	5	0	84	73
<i>Cereus giganteus</i>	2	1	0	0	0	1	5	1	0	0	65	1
<i>Cercidium microphyllum</i>	12	5	0	0	0	5	28	29	3	5	78	1
<i>Echinocereus engelmannii</i>	0	1	0	0	1	0	14	2	0	0	97	1
<i>Encelia farinosa</i>	6	3	0	0	3	0	10	27	0	0	79	15
<i>Ferrocactus acanthoides</i>	1	0	0	0	0	0	21	3	1	0	82	1
<i>Krameria grayi</i>	2	1	0	1	0	0	28	19	3	12	95	20
<i>Larrea tridentata</i>	44	18	2	1	2	15	173	64	9	15	99	23
<i>Lycium</i> spp.	2	1	0	0	1	0	9	10	0	2	50	10
<i>Mammalaria microcarpa</i>	4	0	0	0	0	0	28	3	0	0	95	1
<i>Opuntia acanthacarpa</i>	56	3	0	2	0	1	126	69	5	5	89	1
<i>Opuntia bigelovii</i>	0	0	0	0	0	0	52	16	2	0	88	1
<i>Olneya tesota</i>	0	0	0	0	0	0	1	3	0	0	100	1
<i>Opuntia leptocaulis</i>	1	0	0	0	0	0	5	2	0	2	100	15
<i>Prosopis juliflora</i>	1	0	0	0	0	0	3	0	2	0	100	73

¹Species represented by only one or two plants were omitted. They include *Briekellia coulteri*, *Castilleja*, and *Ziziphus obtusifolia* all of which were present only on the resurvey, and *Opuntia phaeoantha* which was present only on the original survey.

²The mean values were often accompanied by large standard errors. Reliability increases with N1, but even with large N1 and small standard error, multiple populations may be present. *A. deltoidea* for example, was almost always 100% consumed unless completely skipped. Rather than indicating that individual plants were usually only partially consumed, the value of 73% indicates that about 27% of the plants were skipped.

support Grime's hypothesis that succession in stressful environments will progress from ruderal to tolerant strategies among the species present in the community (Grime 1979). Species richness changed very little at either site, and diversity decreases on transects were balanced by increases in plots (Table 2).

Changes in community composition were greatest at Saguaro where seven species disappeared and eight species appeared between surveys (Tables 1 and 3). Added species accounted for 9% of the total number

of plants recorded on the Saguaro resurvey. Five added species accounted for 29% of the resurvey number of plants in Saguaro plots. Most of the added plants were of two species, *C. covesii* and *Castilleja*, both of which exhibit some ruderal characteristics, including rapid dispersal and growth, and presumably relatively short life spans. Three new species were recorded at Dead Man Wash during the resurvey, and two former species disappeared. Numbers of these plants were quite low, however, and most represented less than one percent of the total pre-fire density.

Table 2. Community values for the survey (A) and resurvey (B) for both Saguaro, and Dead Man Wash.

	¹ Density		² Richness		³ Diversity	
	A	B	A	B	A	B
Dead Man Wash						
Plots	68	14	16	17	.44	.56
Transects	11	4	12	10	.78	.71
Saguaro						
Plots	33	23	14	13	.51	.64
Transects	25	25	24	25	.69	.56
Both Sites						
Plots	-	-	19	17	-	-
Combined	-	-	26	31	-	-

¹Plants per 100 m²

²Number of species.

³Evenness, the ratio of the Brillouin index to H(maximum). Natural logs were used.

Recovery of the Dead Man Wash site is proceeding much more slowly than recovery at Saguaro. The reason for this is uncertain. Burning intensity might have been responsible, but this seems unlikely, because kill and consumption were generally higher at Saguaro, and resistance was higher at Dead Man Wash. It seems likely that non-fire factors such as pre- or post-fire drought are responsible for the differences.

CONCLUSIONS AND RESEARCH NEEDS

Although it appears that adaptations to fire are present, they are not strongly developed, and the time for return to pre-fire conditions will be long. At the rate of development observed so far, the Saguaro site would reach original total density after about 5 years, but Dead Man Wash would require 20 years. Original species composition of the sites, assuming this to be a realistic goal (see White 1979), would require many decades to

Table 3.--Saguaro observations of numbers of plants on both surveys (N1 and N2), numbers of plants resprouting (RS1 and RS2) on each survey, numbers of seedlings and resistant plants, and mean kill and consumption percents.

¹ Species	Burned plots						Burned plots and transects					
	N1	N2	RS1	RS2	Seedlings	Resistant	N1	N2	RS1	RS2	%Kill	%Consump.
<i>Acacia constricta</i>	12	5	7	3	0	2	19	19	13	6	94	20
<i>Acacia gregii</i>	4	3	3	3	0	0	4	5	3	4	100	47
<i>Ambrosia deltoidea</i>	209	103	0	0	88	15	535	509	0	1	90	90
<i>Argythamnia neomexicana</i>	0	0	0	0	0	0	0	3	0	0	--	--
<i>Beloperone californica</i>	0	4	0	0	4	0	0	4	0	0	--	--
<i>Brickellia coulteri</i>	0	0	0	0	0	0	4	1	0	0	50	39
<i>Cassia covesii</i>	0	39	0	0	39	0	0	63	0	0	--	--
<i>Calliandra eriophylla</i>	0	0	0	0	0	0	22	12	15	12	100	74
<i>Canotia holocantha</i>	0	0	0	0	0	0	4	1	0	0	0	0
<i>Castilleja</i>	0	10	0	0	10	0	0	16	0	0	--	--
<i>Cercidium microphyllum</i>	4	5	0	0	5	0	24	10	4	1	92	11
<i>Echinocereus engelmannii</i>	2	0	0	0	0	0	6	1	0	0	100	1
<i>Encelia farinosa</i>	0	11	0	0	11	0	18	133	0	1	61	8
<i>Ephedra</i>	11	1	0	0	1	0	52	19	1	5	98	53
<i>Fouquieria splendens</i>	1	0	0	0	0	0	5	1	0	0	100	1
<i>Krameria grayi</i>	9	5	3	3	0	2	86	54	17	29	97	67
<i>Larrea tridentata</i>	9	7	5	0	1	6	76	58	9	6	93	45
<i>Lycium</i>	12	10	7	3	2	5	33	36	9	21	100	51
<i>Mammillaria microcarpa</i>	0	0	0	0	0	0	3	0	0	0	67	1
<i>Opuntia acanthacarpa</i>	23	0	0	0	0	0	65	9	0	0	97	3
<i>Opuntia biglovii</i>	3	0	0	0	0	0	56	18	0	0	98	1
<i>Opuntia leptocaulis</i>	10	1	0	0	0	1	28	4	0	0	96	6
<i>Prosopis juliflora</i>	0	0	0	0	0	0	36	0	0	0	97	34
<i>Simmondsia chinensis</i>	0	0	0	0	0	0	27	14	4	12	96	42

¹To save space, species represented by only one or two plants were omitted from this table. They include one unknown species present on the original survey, *Cereus giganteus*, *Celtis pallida*, and *Olneya tesota*, also present only on the original survey, *Dyssodia porophylloides*, *Ferrocactus acanthoides*, *Mullenbergia porteri*, *Thamnosma montana*, present only on the resurvey, and *Gutierrezia sarothrae* which was present on both surveys.

²See the second footnote to Table 1.

develop. Obviously, no community can be adapted to fires that occur more frequently than the period required for the community to replace the majority of its original species in their former proportions. In 1979 Dead Man Wash returned, again from an ignition point near the highway. The new burn is larger, and contains fewer skips than the 1974 burn. Depending on the relative importance of dispersal of seeds from surrounding, unburned sites, and upon the general success of reproduction, recovery may be slower than after the 1974 fire. Opportunity for soil loss and site degradation (Vogl 1977) is high.

We consider the data made available by this study to be too limited in scope and quantity to yield firm conclusions about natural fire frequency. Too much variability exists between sites to consider the data representative of much of the Desert, and observation time has been too brief for generalizations about recovery rates. Based on the slow recovery rate observed at Dead Man Wash, however, a recommendation for conservative attitudes toward Desert fire management may be appropriate.

In this exploratory analysis a qualitative judgement was made regarding the adaptive characteristics of individual species. Further analysis to define life history traits, including longevity, reproduction, seed sources, phenology, and others, would assist in predicting the progress of succession (Slatyer 1977, Catellino et al. 1979).

The relationship between annual plants and fire requires analysis. At Dead Man Wash the post-fire annual community was diverse, but was generally dominated by introduced species, especially *Erodium cicutarium*. At Saguaro, another introduced annual, *Bromus rubens*, appeared dominant. Does fire lend a competitive advantage to some species, and, as in the Great Basin Desert, do these species support increased fire frequency (Young and Evans 1973)? Do native annuals alone reach densities great enough to carry fire, or must introduced species be present? Perhaps no fire in the Sonoran Desert has been natural since the introduction and spread of exotic annuals. Both frequency and intensity may have increased.

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