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VEGETATION CHANGE IN RESPONSE TO EXTREME EVENTS: THE EFFECT OF A SHORT INTERVAL BETWEEN FIRES IN CALIFORNIA CHAPARRAL AND COASTAL SCRUB[1]

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Abstract. This study describes changes in the abundance of shrub species after two fires in 1979 and 1980 on Otay Mountain in San Diego County, California. The 1979 fire burned a large area of dense chaparral and coastal sage scrub. The 1980 fire burned a portion of the 1979 fire area that had been seeded with annual ryegrass (*Lolium multiflorum*) as an erosion protection measure. Changes in the vegetation caused by the 1979 fire alone were similar to those commonly seen in chaparral wildfire, but the reburning of the vegetation in 1980 caused drastic changes in some areas. *Ceanothus oliganthus* was almost completely eliminated from the area of the 1980 burn. *Adenostoma fasciculatum*, the most abundant shrub at the study site, was reduced in density by up to 97%. Even *Xylococcus bicolor*, which normally resprouts with complete success after fire, suffered substantial mortality with reburning. It is concluded that the changes brought about by the 1980 fire will certainly persist for many decades. While sudden shifts in vegetation composition probably occurred without human intervention, we believe that human activity, especially after the introduction of aggressive annual grasses 200 yr ago, has caused an increase in the instances of abrupt change.

Key words: chaparral; coastal sage scrub; fire; plant life histories; succession; vegetation change.

INTRODUCTION

It is now widely recognized that traditional successional theory is burdened by the assumption of equilibrium. The terms "disturbance" and "perturbation" both imply disruption from equilibrium. Succession has been thought of as recovery toward equilibrium. While equilibrium concepts are fundamental, our understanding of vegetation change would be improved if we made explicit the widely held perception that equilibrium is a special case.

The need is especially acute in arid regions, which exhibit patterns of vegetation change that do not conform in a very useful way with the traditional views. In fire-prone scrub vegetation it is considered that there is "succession after fire" (e.g., Hanes 1971, Purdie and Slatyer 1976), but it is also generally held that fire normally produces little compositional change in the vegetation (Hanes 1971). This and other contradictions in successional theory as applied to arid vegetation could be eliminated if concepts recognized that vegetation is always in a process of change because of variation in environmental fluxes and events of many kinds and magnitudes. Of particular importance are extreme events that cause a sudden shift in species composition or relative importance. Such events, even if of low frequency, can be major factors structuring ecosystems.

We consider fire to be an extreme event in the chaparral, even though it has a relatively high frequency of occurrence, because it brings about many sudden changes, such as the germination of seeds that would otherwise be dormant. It is true that despite the dramatic changes in relative abundance of species caused by chapparal fire, single fires rarely result in local extinction except at the smallest spatial scale. However, historical pattern of fire is important, and adjacent areas with different fire histories can have discernably different vegetation.

In this paper we describe a sudden shift in the composition of southern California shrub vegetation caused by two fires in the same area in <1 yr. Together these fires may be considered a kind of compound extreme event. Human activities played a decisive role in bringing about the events, but that does not diminish the significance of the changes they caused. We believe that similar drastic changes probably occurred with lower frequency before man appeared. In the present human-dominated landscape of southern California, it seems possible that a substantial part of the vegetation pattern in native shrublands can be accounted for by unusual fire patterns of the kind we describe.

THE ECOLOGICAL SETTING

The study was conducted on Otay Mountain in San Diego County, in the Mediterranean climatic zone of southern California (32+37′N, 116°50′W). Although 27 km from the Pacific Ocean, Otay Mountain (elevation 1087 m) is the first major topographic rise encountered by the prevailing westerly winds. It receives considerably more precipitation than the surrounding lowlands and is frequently blanketed by fog. Based on records from adjacent weather stations, the precipitation at the study sites, which range in elevation from 240 to 470 m, probably averages ≈500 mm. The vegetation of the mountain grades from coastal sage scrub and annual grassland at its base to dense evergreen

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TABLE 1. Characteristics of paired sample sites. Transect lengths are combined totals for the portions of each sample site burned in 1979 only and in 1979 and 1980.

Site	Elevation (m)	Slope (%)	Aspect	Total transect length (m)	Vegetation before fire
Pio Pico	240	20	North	166	Coastal sage scrub
Powerline	360	40	North	330	Mixed chaparral
Fireline	370	40	East	160	Chamise chaparral
Trucktrail	370	10	Southwest	188	Chamise chaparral
Bellview	470	30	West	160	Chamise chaparral

chaparral locally dominated by *Cupressus forbesii* at the top.

In August 1979, a wildfire, started by an arsonist, burned over 2000 ha of mixed chaparral and coastal sage scrub on the northern flank of the mountain. Ring counts and fire maps suggest that this area had also burned in 1943 and in the 1950s. After the 1979 fire, the California Department of Forestry seeded most of the burned area with annual ryegrass (*Lolium multiflorium*) as part of its statewide emergency revegetation program. Because of near-record precipitation in the 1979–1980 growing season, ryegrass germination and growth were exceptionally good, and a dense stand of ryegrass was produced (Gautier 1981). An arsonist set fire to the lower margin of the seeded area in July 1980 after the grass had dried, and a significant portion of the area of the 1979 fire was reburned. The 1980 fire burned an irregular area leaving sharp boundaries on slope faces which supported relatively homogeneous vegetation before the fire. Paired plots placed across these boundaries allowed analysis of the effects of repeated fire.

Shrub Life Histories

It has long been recognized that chaparral shrubs possess different life history attributes which result in qualitatively and quantitatively distinctive modes of postfire regeneration. Two life history types have been emphasized in the chaparral literature: obligate seeders and sprouters (Jepson 1939, Wells 1969, Hanes 1971). Obligate-seeding species suffer complete mortality with fire and therefore are dependent on seed reserves to recover after fire. Sprouting species, as the name implies, reestablish after fire by sprouting and may or may not have a significant seed reserve.

Species within the sprouter category fall into two subgroups based on whether they establish seedlings after fire: (1) the "sprouter-nonseeders," and (2) the "sprouter-seeders" (Naveh 1975, Zedler 1977, 1981). A further division of these subgroups can be made based on whether species resprout with nearly complete success after fire (fire resilient) or suffer significant mortality (fire sensitive).

It is also possible to identify a distinctive group of life history features associated with coastal sage species. Zedler (1977) describes this life history type as having: (1) reduced sprouting ability, with the degree of resprouting very sensitive to fire intensity, and (2) high production of seeds that do not require fire stimulation for germination. Presentation of results on the effects of fire on shrub abundance is organized around this expanded classification scheme.

Methods

Paired plots were established at five sample sites along the 1980 burn perimeter (Table 1). Each paired plot consisted of one plot in the area burned in 1979 only (burned once) and one plot in the area burned in 1979 and 1980 (burned twice). One-metre wide belt transects were laid out along the slope contour at each site. The number and lengths of transects were the same between paired portions of a single site but varied among the sites.

The initial samples were taken in January and February 1981 except at the Powerline site, which was sampled in May 1981. The transects sampled in January and February were reexamined in May 1981 to determine whether additional seedling establishment or resprouting had occurred. This resulted in changes in the data only for *Xylococcus bicolor*.

Both density and frequency were measured for mature shrubs and shrub seedlings. Data on mature shrubs were recorded in each of four quarters of consecutive 1×1 m quadrats along the belt transect. Because seedlings tended to be more numerous than mature shrubs, seedling abundances were recorded in only the lower left quarter of each 1-m^2 quadrat. At the Powerline site seedling abundances were low and were recorded in all four quarters. Plants were tallied only if they were rooted in the sampling area. Nomenclature follows Munz (1974).

Density counts in terms of numbers of individuals could not be obtained for sprouting species (except *Adenostoma fasciculatum*) because it was impossible to determine the correspondence, if any, between clumps of stems and genetic individuals. While density was calculated for those species for which it was possible, frequency and change in frequency are the only data that apply to all species and life forms. Mortality for both sprouting and nonsprouting species can be assessed by the ratio of pre- and postfire frequency. Since this ratio measures change in area occupied, it

TABLE 2. Mature-shrub abundances before the 1979 fire. Frequencies are the proportion of quadrats in which a species was present. Species at each site are arranged alphabetically. Density counts are not given for certain sprouting shrubs because it was not possible to determine whether clumps of these species were single genetic individuals. Dash indicates that density could not be calculated. N/P means not present.

Site / Species	Burned 1979 only		Burned 1979–1980	
	Frequency (%)	Density (no./m² ± 1 SE)	Frequency (%)	Density (no./m² ± 1 SE)
Pio Pico				
Artemisia californica	4.9	0.22 (±0.06)	5.2	0.26 (±0.06)
Eriogonum fasciculatum	4.3	0.13 (±0.05)	2.4	0.10 (±0.03)
Salvia apiana	5.2	0.21 (±0.05)	12.9	0.45 (±0.09)
Powerline				
Adenostoma fasciculatum	7.3	0.29 (±0.01)	7.4	0.35 (±0.01)
Cercocarpus minutiflorus	1.8	—	0.5	—
Heteromeles arbutifolia	3.3	—	4.0	—
Keckiella cordifolia	6.1	—	3.4	—
Lonicera subspicata	2.2	—	0.9	—
Rhamnus crocea	2.2	—	2.6	—
Rhus laurina	2.8	—	1.1	—
Xylococcus bicolor	3.9	—	5.9	—
Fireline				
Adenostoma fasciculatum	18.4	0.93 (±0.13)	27.2	1.48 (±0.16)
Xylococcus bicolor	18.4	—	13.1	—
Trucktrail				
Adenostoma fasciculatum	19.1	1.00 (±0.11)	24.2	1.47 (±0.16)
Xylococcus bicolor	3.5	—	4.5	—
Bellview				
Adenostoma fasciculatum	22.5	1.15 (±0.23)	25.0	1.51 (±0.40)
Ceanothus oliganthus	5.9	0.29 (±0.07)	2.8	0.15 (±0.04)
Xylococcus bicolor	3.1	—	N/P	—

can be argued that it is a more meaningful expression of population change for plants than are those based on density.

Because all shrubs at the five sample sites were burned by the 1979 fire, only two categories were needed to describe the condition of mature shrubs encountered in plots burned by the 1979 fire only: (1) killed by the 1979 fire, and (2) sprouting after the 1979 fire. Remains of shrubs that died before the 1979 fire were completely consumed by the fire and do not affect estimates of fire-caused mortality.

Unlike the 1979 brush fire, the 1980 grass fire left small unburned patches within its perimeter. In plots burned by the 1979 and the 1980 fires, shrubs that were burned only by the 1979 fire were so noted and recorded as either (1) killed by the 1979 fire or (2) sprouting after the 1979 fire. Shrubs that were burned by both fires were recorded as either (1) killed by the 1979 fire, (2) killed by the 1980 fire, or (3) sprouting after the 1980 fire. Shrubs killed by the 1980 fire could be distinguished from those killed by the 1979 fire by the presence of burned sprouts, which were clearly different from the larger stems killed by the 1979 fire. Burned shrubs were identified to species on the basis of stem morphology, bark texture, and wood color and grain.

While some seedlings may have been present in the vegetation before the 1979 fire, densities were probably very low (Keeley 1973, Biswell 1974, Parsons 1976, P. H. Zedler, *personal observation*) and survival through the intense 1979 brush fire unlikely. Therefore, we assumed that all seedlings encountered during sampling had established after fire. In areas burned by both the 1979 and 1980 fires, live seedlings were recorded as either (1) resprouting after the 1980 fire or (2) established after the 1980 fire.

RESULTS

Obligate seeder: Ceanothus oliganthus

Ceanothus oliganthus, a relatively common shrub in the more mesic low-elevation (100–180 m) chaparral of southern California, was the only obligate-seeding species sampled in the study. It occurred only at the Bellview study site, where it was the second-most-abundant shrub before the 1979 fire (Table 2).

The effect of the 1979 fire.—Following the typical pattern for obligate-seeding shrubs, all individuals were killed by the 1979 fire (Table 3), and numerous seedlings were established in the 1st yr after fire from seed stored in the soil (Table 4). Seedling density after the 1979 fire was more than 40 times the density of mature shrubs before fire.

The effect of reburning.—The situation was very different after the 1980 grassfire. All seedlings within

TABLE 3. Mortality of mature shrubs as a result of the 1979 fire, and mortality of shrubs sprouting after the 1979 fire as a result of the 1980 fire. Total mortality of mature shrubs as a result of both fires is also shown. Values are computed from density estimates for those species for which density could be recorded. Frequency counts are used otherwise. The following species, omitted from the table for brevity, were observed in the sample plots but showed no mortality from either fire: *Cercocarpus minutiflorus*, *Heteromeles arbutifolia*, *Keckiella cordifolia*, *Lonicera subspicata*, *Rhamnus crocea*, and *Rhus laurina*. In this list, only *Rhus laurina* is known to establish seedlings in abundance after fire. Dash indicates that values are not relevant or could not be calculated. N/P means not present.

		Percent mortality resulting from		
Species	Site	1979 fire*	1980 fire†	Both fires†
Adenostoma fasciculatum	Powerline	55	67	83
	Fireline	43	72	84
	Trucktrail	85	85	97
	Bellview	79	93	99
Artemisia californica	Pio Pico	>95	—	>96
Ceanothus oliganthus	Bellview	100	—	100
Eriogonum fasciculatum	Pio Pico	100	—	100
Salvia apiana	Pio Pico	52	12	67
Xylococcus bicolor	Powerline	4	17	20
	Fireline	0	31	31
	Trucktrail	5	22	22
	Bellview	0	N/P	—

* Values are means computed from percent mortality recorded in the once-burned and the twice-burned portions of the paired sample sites.

† Values are computed from data gathered only in the twice-burned portion of paired sample areas.

the portion of the Bellview study site burned in the 1980 fire were destroyed with the exception of those in isolated unburned patches (Table 4). By destroying most of the seedlings, the second fire reduced *C. oliganthus* to a negligible density within the 1979–1980 fire area (Table 4). Complete extinction of *C. oliganthus* within the perimeter of the 1980 fire was prevented only by the failure of the fire to burn small patches of ground with light grass cover. A similar degree of reduction of the obligate seeder *C. cuneatus* in a grassfire was reported by Hedrick (1951).

Sprouter-seeder, fire sensitive: Adenostoma fasciculatum

Adenostoma fasciculatum is probably the most abundant of all chaparral shrubs (Hanes 1977). It occurs throughout the chaparral region from Oregon to Baja California, often in nearly pure stands. A number of studies have shown that after fire *A. fasciculatum* both sprouts and establishes seedlings from seed present in the soil (Sampson 1944, Hedrick 1951, Horton and Kraebel 1955, Keeley 1973). *A. fasciculatum* occurred at four of the paired sample sites in our study area and was the most abundant shrub.

The effect of the 1979 fire.—The 1979 fire caused considerable mortality of mature shrubs (Table 3). Percent mortality values at two of the paired sites, Bellview and Trucktrail, are high compared with values in the literature, many of which are from studies done in northern California (Sampson 1944, Hedrick 1951, Horton and Kraebel 1955). For example, Hedrick (1951) presents data for an *A. fasciculatum* stand in Lake County burned in 1945, in which mortality of mature chamise was only 31%. At our study sites *A. fasciculatum* mortality rates for the relatively mesic Fireline and Powerline sites are considerably lower than those for the Bellview and Trucktrail sites, which have westerly and southeasterly exposures, respectively (Table 3), and presumably are more drought prone. This drought stress-resprout vigor correlation which seems to exist on Otay Mountain may be a local expression of a general tendency for resprouting to be less successful and obligate seeding to be more prevalent with increasing aridity in the entire chaparral zone (Keeley 1977). Reduced sprouting on the drier sites may be due to reduced carbohydrate reserves, as suggested by Laude et al. (1961). Alternatively, lower fuel moisture on drier sites may result in hotter fires, which decrease resprouting by killing more of the meristematic tissue in the burl.

A. fasciculatum seedling establishment was high after the 1979 fire (Table 4). Considering both seedlings and resprouting shrubs, the 1979 fire increased the density and frequency of *A. fasciculatum* at all sites at which it occurred (Table 5).

The effect of reburning.—The 1980 fire reduced the abundance of *A. fasciculatum* at all paired sample sites, by killing many mature resprouting shrubs and by destroying nearly all seedlings established after the 1979 fire. The mortality of the mature shrubs varied but was high at all sites (Table 3). The Bellview and Trucktrail sites again showed the greatest losses.

As with *C. oliganthus*, the only seedlings which survived within the perimeter of the 1980 fire were those in isolated unburned patches (Table 4). Considering both seedlings and resprouting shrubs, repeated fire reduced *A. fasciculatum* abundances (Table 5) by ≈50–95%. At the Bellview site the reduction approaches a local extinction.

Two other studies in California have also reported high mortality of both seedlings and sprouts of *A. fasciculatum* from grassfires. In San Bernardino County, D. R. Cornelius (*personal communication*) found 100% mortality of seedlings and 94% mortality of sprouts in an area seeded with grass and mustard in the first season of recovery from fire and burned the following summer. Hedrick (1951) examined *A. fasciculatum* in Lake County burned in the 1st, 2nd, and 3rd yr of recovery. For sprouts he found 77, 24, and 34% mortality, respectively. For seedlings the mortality rates were 99, 98, and 100%. His data suggest that sprouting plants, but not seedlings, quickly lose hypersensitivity to fire.

TABLE 4. Shrub seedling densities after fire. Values in parentheses are standard errors of the mean. The following species were present as mature plants but not as seedlings in either burn area: *Cercocarpus minutiflorus*, *Heteromeles arbutifolia*, *Lonicera subspicata*, *Rhamnus crocea*, *Rhus laurina*, and *Xylococcus bicolor*.

Species	Site	Shrub seedling density (no./m²)	
		After the 1979 fire*	After the 1980 fire†
Adenostoma fasciculatum	Powerline	1.65 (±0.12)	0.16 (±0.05)
	Fireline	22.16 (±2.89)	0.60 (±0.40)
	Trucktrail	10.24 (±1.53)	0.04 (±0.10)
	Bellview	2.20 (±0.51)	<0.05 ‡
Artemisia californicum	Pio Pico	2.62 (±0.30)	0.39 (±0.12)
Ceanothus oliganthus	Bellview	12.04 (±1.48)	<0.05
Eriogonum fasciculatum	Pio Pico	0.01 (±0.01)	<0.01
Keckiella cordifolia	Powerline	0.01 (±0.003)	0.005 (±0.004)
Mimulus sp.	Powerline	0.05 (±0.01)	0.001 (±0.001)
Ribes indecorum	Powerline	0.02 (±0.01)	0.0
Salvia apiana	Pio Pico	0.04 (±0.03)	0.01 (±0.01)

* Values are computed from data gathered in portions of paired sample sites burned in 1979 only.
† Values are computed from data gathered in portions of paired sample sites burned in 1979 and 1980.
‡ Abundance estimates preceded by a < sign indicate that seedlings were observed but were not encountered in the sample. The number given is the density that would be obtained if only one seedling were present in the sample.

Sprouter-seeder, fire resilient: Keckiella cordifolia *and* Rhus laurina

Keckiella cordifolia is a subshrub which is widely distributed but never more than very locally dominant. In our study area, it was present only at the Powerline site, where it was unusually abundant (Table 2). Mature *K. cordifolia* shrubs apparently have considerable capacity to withstand fire since neither the 1979 nor the 1980 fires caused any mortality.

Seedlings were observed in both the once- and twice-burned areas (Table 4). Because *K. cordifolia* flowered in the first season of recovery (i.e., early summer 1980), we cannot say if the seedlings were produced from seeds present in the soil before the 1979 fire or from seeds produced after the fire. We suspect the latter, but in either case, *K. cordifolia* appears to have a remarkable ability to increase population numbers after repeated burning (Table 5).

Rhus laurina is a common shrub at lower elevations in the chaparral and coastal sage scrub of southern California. It occurred at several of the paired sample sites, but it was present in abundance only at the Powerline site (Table 2). *R. laurina* is recognized as a sprouter-seeder (Zedler 1977, 1981). Seedlings typically establish in moderate abundance in the 1st yr after fire, and it was surprising that no *R. laurina* seedlings were found at any of the study sites. The 1979 and 1980 fires caused no mortality of the mature individuals present before fire (Table 3), so that there was no net effect of either fire on *R. laurina* abundance (Table 5).

Sprouter non-seeder, fire sensitive: Xylococcus bicolor

Xylococcus bicolor is a locally abundant chaparral shrub found at lower elevations in extreme southern California and Baja California. *X. bicolor* occurred at four of the sample sites in our study area (Table 2).

Mature *X. bicolor* resprouts vigorously after fire but does not seem to establish seedlings (Zedler 1981). As a result, the 1979 fire had little effect on *X. bicolor* abundance. Reburning, however, did result in substantial change in the abundance of *X. bicolor*. Living *X. bicolor* stems were present in fewer quadrats after the 1980 fire than before the fire (Table 3). In some cases this was the result of death of only part of a plant which had been present in a quadrat prior to fire, but in others, entire isolated clumps of *X. bicolor*, presumably genetic individuals, failed to resprout. Since no seedlings were present in the twice-burned portion of the study sites, the net effect of the 1980 fire was to reduce the abundance of *X. bicolor* by up to nearly one-third (Table 3).

Sprouter non-seeder: fire resilient

Three species encountered at the Powerline study site, *Cercocarpus minutiflorus*, *Heteromeles arbutifolia, and Rhamnus crocea*, are similar to *X. bicolor* in the ability of mature plants to sprout vigorously after fire and the apparent inability to establish seedlings in 1st-yr burns. Unlike *X. bicolor*, however, repeated burning had no measurable effect on abundance of these species. All quadrats that contained living stems before fire contained resprouts after both the 1979 and 1980 fires. *C. minutiflorus* may be an exception. On a west-facing slope, outside the sample area near the Powerline study site, the 1980 fire severely reduced the size of several clumps of *C. minutiflorus* and completely killed others. No seedlings of any species in this group of shrubs were established after either the 1979 or the 1980 fires (Table 4).

Coastal sage species

Three shrubby species commonly associated with the coastal sage scrub, *Artemisia californica*, *Eriogonum fasciculatum*, and *Salvia apiana*, dominated the

TABLE 5. Postfire abundance for mature shrubs and seedlings combined, expressed as a proportion of pre-1979 fire mature shrub abundance. Estimates are based on data from the 1/4-m² quadrat sample in which both mature shrubs and seedlings were recorded. Discrepancies between values in this table and previous tables are due to the use of data from the smaller quadrats. Main table entries are computed from frequency data. Entries in parentheses are computed from density data. N/P means not present.

Species	Site	Burned 1979 only	Burned 1979 and 1980
		Relative abundance (postfire/prefire)	
Adenostoma fasciculatum	Powerline	2.14 (6.10)	0.29 (0.64)
	Fireline	3.00 (24.41)	0.29 (0.56)
	Trucktrail	2.91 (10.00)	0.16 (0.06)
	Bellview	1.06 (2.10)	<0.04 (<0.03)*
Artemisia californica	Pio Pico	9.20 (12.00)	0.78 (1.50)
Ceanothus oliganthus	Bellview	24.67 (41.52)	<0.25 (<0.33)
Cercocarpus minutiflorus	Powerline	1.00	1.00
Eriogonum fasciculatum	Pio Pico	<0.50 (0.08)	<0.25 (<0.10)
Heteromeles arbutifolia	Powerline	1.00	1.00
Keckiella cordifolia	Powerline	1.33	1.15
Lonicera subspicata	Powerline	1.00	1.00
Rhamnus crocea	Powerline	1.00	1.00
Rhus laurina	Powerline	1.00	1.00
Salvia apiana	Pio Pico	1.20 (0.67)	0.11 (0.33)
	Powerline	1.00	0.83
	Fireline	1.00	0.64
	Trucktrail	1.00	0.25
Xylococcus bicolor	Bellview	1.00	N/P

* Proportions preceded by a < sign indicate that individuals were present but were not encountered in the sample. The number given is the proportion that would be obtained if only one individual was present in the sample.

vegetation at the Pio Pico study site prior to the 1979 fire (Table 2). The species had different responses to burning. Only *S. apiana* resprouted with much success after the 1979 fire (Table 3). None of the *A. californica* or *E. fasciculatum* sampled had resprouted, although a few *A. californica* were observed to be resprouting in surrounding areas.

Seedlings of all three species appeared after the 1979 fire (Table 4). The density of seedlings of *A. californica* was more than an order of magnitude greater than that of mature individuals present before the 1979 fire (Table 5). This increase must be interpreted with caution, however, since the relatively soft-wooded stems of coastal sage species have a tendency to burn more completely than the stems of chaparral species, and we may have underestimated their abundance before the 1979 fire.

Fewer seedlings of *S. apiana* and *E. fasciculatum* were present. Considering both shrubs and seedlings together, the 1979 fire reduced the density of *S. apiana* by 33% and that of *E. fasciculatum* by 90% (Table 5).

The three coastal sage scrub species also responded differently to reburning. Abundance of *E. fasciculatum* showed little change since it was already extremely low as a result of the 1979 fire. No seedlings were observed anywhere in the twice-burned area, suggesting that the 1980 grassfire destroyed seedlings that had established after the 1979 fire.

The 1980 fire resulted in mortality of *S. apiana* shrubs, but the percent reduction in density was lower than that caused by the 1979 fire (Table 3), a reverse of the response exhibited by other sprouters which suffered the same or higher mortality with the 1980 reburn. Considering both mature shrubs and seedlings, repeated burning reduced density by 67% (Table 5).

Because *A. californica* showed little tendency to resprout after the 1979 fire, almost all the *A. californica* present at the Pio Pico study site were seedlings. Surprisingly, some seedlings were able to resprout after the 1980 fire, and therefore of all the species observed, *A. californica* seedling populations were the least affected by reburning. Comparison of seedling density in the paired plots shows that ≈15% of the seedlings resprouted after the 1980 fire. Comparison of preburn heights of resprouting seedlings in the burned area and of seedling heights in the unburned area showed that larger seedlings survived reburning more successfully. Because of seedling survival, *A. californica* increased in absolute abundance relative to pre-1979 fire density despite reburning (Table 5) and therefore increased even more in relative abundance. High rates of survival of *A. californica* seedlings in grassfires have been reported for other areas in California.

Responses of species of other growth forms

Although we recorded data on all vascular plant species encountered in the sampling, we did not analyze quantitative population changes in the herbs and subshrubs. However, certain general trends were obvious. After the 1979 fire, and despite the seeding of ryegrass, the spontaneous introduced annuals such as

Bromus rubens, *Avena* spp., and *Erodium cicutarium* were abundant. Since the annual herbaceous cover was noticeably sparser in the area of the 1980 burn, it is probable that many of the seeds produced in the spring of 1980 were killed by the 1980 fire. Despite this, all of the species abundant in the portion of the study sites not burned in 1980 also appeared in the spring of 1981 in the area of the grassfire. Some subshrubs, most notably *Eriophyllum confertiflorum*, *Helianthemum scoparium*, and *Lotus scoparius*, which had germinated abundantly after the 1979 fire, suffered heavy mortality in the 1980 fire. Seedlings of these species were not apparent in 1981 in the area of the grassfire, but since they commonly occur in disturbed areas, rapid invasion or expansion from the few remaining plants might be expected. Native perennial herbs such as *Dichelostemma pulchella* and *Calochortus weedii*, which possess corms deep in the soil, suffered very little from the 1980 fire.

Vegetation change after fire

Overall vegetation change is most conveniently measured by changes in frequency, since this affords a means of comparing clonal and nonclonal species. An increase in the frequency of empty quadrats may be interpreted as a decline in the occupancy of the site.

For nearly all shrub species at all the study sites, the 1979 fire caused either an increase or no change in frequency (Table 6). Only *E. fasciculatum* suffered a slight decline. The greatest increases were a result of high rates of seedling establishment. This accounts for the large increase of *C. oliganthus* (an obligate seeder) and the more modest increases of *A. fasciculatum* and *A. californica*. As expected, sprouter nonseeders showed little change.

In contrast, a large number of species suffered substantial declines in frequency as a result of the 1980 fire. The most sensitive species included *C. oliganthus*, *A. fasciculatum*, and *S. apiana*, all of which depend to a large degree on successful seedling establishment for population replacement after fire. Surprisingly, even a sprouter nonseeder, *X. bicolor*, was adversely affected. Where these sensitive species were abundant before the 1979 fire, such as at the Bellview, Trucktrail, and Fireline study sites, large changes in vegetation composition occurred as a result of reburning. Where less sensitive shrub species predominated, as at the Powerline study site, change in vegetation composition and site occupancy was minimal.

TABLE 6. Frequencies (i.e., percentage of quadrats in which individuals were present) of the shrub species at each site before and after fire. Frequencies of quadrats which contained no shrubs ("empty quadrats") are also shown. N/P means not present.

Site / Species	Burned 1979 only		Burned 1979 and 1980	
	Before 1979 fire	After 1979 fire	Before 1979 fire	After 1980 fire
	Frequency (% of quadrats)			
Pio Pico				
Artemisia californica	5	46	9	7
Eriogonum fasciculatum	2	<1	4	<1
Salvia apiana	5	6	9	1
Empty quadrats	88	54	79	92
Powerline				
Adenostoma fasciculatum	7	15	7	2
Cercocarpus minutiflorus	2	2	1	1
Heteromeles arbutifolia	3	3	4	4
Keckiella cordifolia	6	8	3	4
Lonicera subspicata	2	2	1	1
Mimulus sp.	0	4	0	1
Rhamnus crocea	2	2	3	3
Ribes sp.	0	2	0	0
Rhus laurina	3	3	1	1
Xylococcus bicolor	4	4	6	5
Empty quadrats	69	55	72	76
Fireline				
Adenostoma fasciculatum	25	76	31	9
Xylococcus bicolor	16	16	11	7
Empty quadrats	60	11	56	87
Trucktrail				
Adenostoma fasciculatum	22	64	25	4
Artemisia californica	N/P	18	N/P	2
Xylococcus bicolor	4	4	4	1
Empty quadrats	73	23	69	92
Bellview				
Adenostoma fasciculatum	23	24	28	<1
Ceanothus oliganthus	3	74	4	<1
Xylococcus bicolor	5	5	N/P	N/P
Empty quadrats	73	21	69	>99

DISCUSSION

The 1979 fire produced the effects well known from other studies of chaparral wildfire (e.g., Cooper 1922, Sampson 1944, Horton and Kraebel 1955). Gaps were created by the death or partial reduction of some mature individuals, and these gaps were recolonized by seedlings and to a minor extent by the vegetative spread of resprouts. The relative abundance of the species after the 1979 fire was different from the prefire condition, but fire-free vegetation development will likely result in a return to about the same composition and structure.

Disruption of the postfire vegetation by the short interval between the 1979 and 1980 fires drastically changed relative abundances of shrub species. The soil seed reserves were depleted by germination in spring 1980. Seed production, even by resprouts, had not yet begun for most species and certainly not for any of the dominant species. As shown by the frequency data (Table 6) the effect was to enlarge the gaps in the shrub matrix and to produce abrupt discontinuities in the vegetation at the margin of the 1979 and 1980 fires.

The response to reburning differed considerably among the species, with the obligate seeder *Ceano-*

thus oliganthus proving, as expected, to be the most sensitive. Some sprouting species also suffered surprisingly high mortality. Since burls (lignotubers) are generally held to be features which enhance survival through fire, it seems odd that *Adenostoma fasciculatum* and *Xylococcus bicolor*, the two species in the study area with well-developed burls, should have suffered more from the grassfire than other sprouting shrubs. This may be because the growing points arising from burls are more exposed or because of the mode of carbohydrate storage associated with a burl structure.

Because of the differences in species responses, some areas were changed more than others. North-facing slopes dominated by vigorous sprouters (other than *Xylococcus bicolor*) came through relatively little affected. In contrast, at the *Adenostoma fasciculatum*-dominated Fireline site, a sharp discontinuity has been created which will be even more obvious as the shrub canopy matures. Overall, the area burned in 1980 is now a conspicuously different phase of the local vegetation.

These local differences in the vegetation will remain for a long time. In order for the 1980 burn area to develop a composition and structure similar to the surrounding vegetation, new individuals of the depleted shrub species will have to become established. This process will be slowed because of relatively limited dispersal and specialized germination requirements, especially for *Ceanothus oliganthus* and *Adenostoma fasciculatum*. Seeds of both these species seem to germinate at high rates only after fires or severe disturbance of the soil surface (Quick and Quick 1961, Christensen and Muller 1975). Without fire, no significant invasion of these species is to be expected. After fire, a modest rate of spread might result.

Dispersal and germination would be less serious problems for some species, especially those of the coastal sage scrub type. Despite a lack of obvious features enhancing dispersal except small seed size, *Artemisia californica, Salvia apiana,* and especially *Eriogonum fasciculatum* are vigorous invaders of man-made and natural disturbance areas. Their success must be attributed primarily to the lack of specialized germination requirements, which allows seedling establishment without fire or surface disruption (Zedler 1977, Westman 1981).

Some of the evergreen sprouting species such as *Heteromeles arbutifolia, Rhamnus crocea, Ribes indecorum,* and *Rhus laurina* have fleshy fruits which are probably animal dispersed. Although seedlings of these species do not seem to have special germination requirements, few seedlings are found in recent burns or other disturbed areas, and we suspect that their rate of invasion would be slow.

Observations made elsewhere in California support our belief that repeated fire can cause sudden and relatively permanent change. The devastating effect of grassfires on shrub seedlings is well known to ranchers and land managers, and burning grass planted in recently burned chaparral is a recommended technique for increasing grass at the expense of brush (Kay 1960, Murphy 1967, Biswell 1974, Emrick and Adams 1977). While few detailed studies of the effect of grassfires on shrublands are available, the evidence supports the ideas that the purposeful application of fire can virtually eliminate some shrub species and that reinvasion by the shrubs is slow.

It seems probable that the sharp vegetation discontinuities produced by the 1980 fire on Otay Mountain will gradually blur but will probably be discernible for a century or more. The gaps created by the 1980 fire mortality will be largely reoccupied but probably by different species than those whose demise created the gaps. Since the lower slopes of Otay Mountain are dominated by a coastal sage vegetation, there will probably be an upward shift of the zone of coastal sage scrub dominance in the area of the 1980 grassfire, with an increase of *Artemisia californica, Salvia apiana,* and *Eriogonum fasciculatum*. The more mesic slopes where sprouting nonseeding species were dominant before the fire should suffer little invasion.

An expansion of herbs and subshrubs is also to be expected. The common pattern after chaparral fires, like that of 1979, is for native and introduced annual herbs to dominate for the 1st yr and then gradually decline as the cover of shrub and subshrubs inceases. Subshrubs, woody only at the base, such as *Eriophyllum confertiflorum, Helianthemum scoparium,* and *Lotus scoparius,* establish in the 1st yr and normally peak in importance 4–8 yr after the fire. While herbs and subshrubs were depleted in the 1980 grassfire, their capacity for invasion and spread in nonfire conditions assures that they will assume much greater relative importance over the next decade. In places they may usurp space to a degree that will further reduce the chance of establishment of chaparral shrub species, especially in the absence of fire. Introduced annual species (e.g., *Bromus rubens, Erodium cicutarium*) are likely to increase most rapidly.

If there is an expansion of coastal sage shrubs and an increase in herbaceous vegetation, the fuel characteristics of the vegetation in the area of the grassfire will be significantly different from the surrounding vegetation burned only in 1979. A future fire could carry through all or part of the relatively fine fuels in the 1980 burn area but stop when it reaches the evergreen chaparral. Given the current plague of wildland arson, it is not unreasonable to expect that some or all of the grassfire area will be reburned before the time that the adjacent chaparral can readily carry a fire. If so, the discontinuity produced by the 1980 fire may be perpetuated and made more emphatic by future fires, rather than being blurred or eliminated.

The fine fuel provided by the planted ryegrass was an important element in the sequence of events that produced the changes on Otay Mountain. Bradbury (1978) provides evidence that equally sudden change can occur without artificial planting. He investigated patches of *Salvia apiana* which occur in a matrix of *Adenostoma fasciculatum* chaparral in eastern San Diego County. He showed that the patches had persisted for at least 100 yr and that they could not be explained by differences in soil or topography. He concluded that the patches date to past fires and that *Salvia apiana* invaded after the elimination of *Adenostoma fasciculatum*. We suspect that two fires in rapid succession, the second in spontaneous vegetation of herbs and subshrubs, may have killed the *A. fasciculatum*. Cover heavy enough to allow a fire to carry in such young vegetation may require greater than normal rainfall. Even in the Sonoran desert of Arizona, two successive years of high rainfall produce enough fine fuels to carry fire (McLaughlin and Bowers 1982).

The pattern that Bradbury recorded, like that on Otay Mountain, developed in a landscape in which human influence is pervasive. Could fires at short intervals have occurred in pre-European times? To answer this question the effect of the introduction of Mediterranean annual grasses must be considered. The native herbaceous flora which occurs after fires in dense chaparral areas is generally too sparse in the 1st yr to carry fire over large areas. With the increase in subshrubs, the cover of fine fuels can become more general. It must certainly have been possible for lightning fires to spread in such purely native vegetation, and we hypothesize that small patches, but perhaps rarely areas as large as that burned in 1980, would have experienced fire at short intervals in the pre-European landscape.

After the introduction of aggressive annual grasses, the probability of fire at short intervals increased. Unlike the majority of native annuals, which flush in the 1st yr and fade quickly, grasses such as *Bromus rubens* persist indefinitely in open patches in the chaparral and create denser and more uniform cover better able to carry fire. They increase with grazing and other disturbances, so that a new vegetation type has emerged: degraded shrublands with an annual-grass understory. Purposeful and accidental fires carried largely by grass have repeatedly burned some areas, and the cumulative effect has been recession of chaparral shrubs and expansion of the coastal sage type, which is capable of dispersing and establishing in chaparral thinned by repeated fire (Oberbauer 1978).

Despite a concerted effort over the last 75 yr to keep the shrub vegetation of southern California in its original condition as watershed protection, we believe that alteration of the fire regime has been causing significant change. We doubt if traditional climax-oriented successional theories can be of much use in predicting the ultimate outcome. Because human activities cause unique disturbances and modify the regime of natural disturbances like fire, there is little reason to expect vegetation stability.

Total vegetation change may be said to consist of sudden shifts in abundance caused by environmental extremes such as fire and gradual change during periods in which "successional" processes operate. Succession theory has concentrated on predicting the rate and direction of change between environmental events. As frequency and intensity of environmental extremes increase, a smaller proportion of total compositional change can be ascribed to processes that occur between extreme events. In the chaparral, and we suspect in arid regions generally, species extinction at any spatial scale is far more likely to be caused by environmental events than by competitive interactions in a disturbance-free environment. In arid regions, special consideration must be given to sequences of events, which can have a strong cumulative effect. We must recognize the importance of differences in the life histories and physiology of species with respect to the variety of possible extreme events. Progress is being made (e.g., Zedler 1977, Noble and Slatyer 1980, Keeley 1981, Noble 1981), but much work still needs to be done. For the present, land managers must recognize that predictions of the outcome of vegetation manipulation made on the basis of existing succession theory must have large margins of error.

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