

Demographic structure of California chaparral in the long-term absence of fire

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Abstract. Demographic structure of 12 chaparral sites unburned for 56 to 120 years was investigated. All sites were dominated by vigorous shrub populations and, although there was colonization by seedlings of woodland tree species in several stands, successional replacement of chaparral was not imminent. Although successional changes in community composition were evident, there was no indication of a decline in species diversity. Non-sprouting species of *Ceanothus* suffered the greatest mortality at most, but not all, sites. Sprouting shrubs, such as *Quercus* and *Heteromeles* had very little mortality, even in stands more than a century old. All postfire resprouting species had multiple stems of different ages indicating these shrubs were capable of continuously regenerating their canopy from basal sprouts. *Ceanothus* populations were highly clumped and there was a significant correlation across all sites between variance/mean ratio and percentage mortality. As *Ceanothus* populations thinned, they became less clumped. In mixed chaparral stands, *Quercus* and *Heteromeles* were significantly taller than associated *Ceanothus* shrubs and overtopped the *Ceanothus*; at two sites, the density of live *Quercus* per plot was correlated with the density of dead *Ceanothus*. Thus, mortality of *Ceanothus* stems is likely related to both intra and interspecific interactions.

Seedling recruitment was observed for most shrub species that regenerate after fire by resprouting; seedling and sapling densities ranging from 1000-36 500 ha⁻¹ were recorded for *Quercus dumosa*, *Rhamnus crocea*, *Prunus ilicifolia*, *Heteromeles arbutifolia* and *Cercocarpus betuloides*. For all but the last species, seedlings and saplings were most abundant beneath the canopy cover and not in gaps. Across all sites, recruitment was significantly correlated with depth and biomass of the litter layer. *Cercocarpus betuloides* was present in several stands, but seedling establishment was found only in one very open, disturbed stand. Regardless of stand age, taxa such as *Adenostoma*, *Arctostaphylos* and *Ceanothus*, which recruit seedlings after fire, had no significant seedling production.

Keywords: Chaparral; Mortality; Resprouting; Seedling recruitment; Vegetative regeneration.

Nomenclature: Munz (1968).

Introduction

California chaparral is widely characterized as a fire-type vegetation because community composition is only briefly altered and many species even require fire for recruitment of seedlings (Sampson 1944; Hanes 1977; Keeley & Keeley 1988).

Some have considered chaparral, in part or all of its range, to be a fire maintained disclimax that, if unburned, would eventually be succeeded by grassland (Sampson 1944) or woodland (Horton 1960; Wells 1962). Pejorative terms such as decadent, senescent, senile, trashy and unnatural are invariably used to describe chaparral that remains unburned for more than 50 yrs (Heady 1974; Hanes 1977; Vogl 1977; Rundel & Parsons 1979; Reid & Oechel 1984; Biswell 1989). This is based on the belief that all chaparral shrubs require fire for seedling establishment and resprouting shrubs require fire for resprouting that rejuvenates the canopy. Older chaparral communities are considered to be unproductive, with little annual growth, to be nutrient limited, with an over-accumulation of allelopathic toxins, and to have reduced species diversity.

These conclusions about older stands of chaparral (Fig. 1), however, are held in question by some (Zedler & Zammit 1989). The belief that chaparral becomes unproductive with age is based on studies of deer browse, which were not valid measures of productivity because production above 1.5 m (deer browse line) was not included (Biswell et al. 1952; Hiehle 1964; Gibbens & Schultz 1963) and much of the growth in older shrubs is above that height. Valid measures of productivity indicate no decrease in productivity up to at least 80 yrs (Rundel & Parsons 1979; Hubbard 1986; Black 1987). There are also good reasons for questioning the idea that old chaparral becomes senescent; Reid (1985) reported that photosynthetic capacity, on a per leaf basis, did not decrease in 80 yr old stands of chaparral. The notion that older stands become nutrient limited has also been questioned (Schlesinger et al. 1982). Evidence that

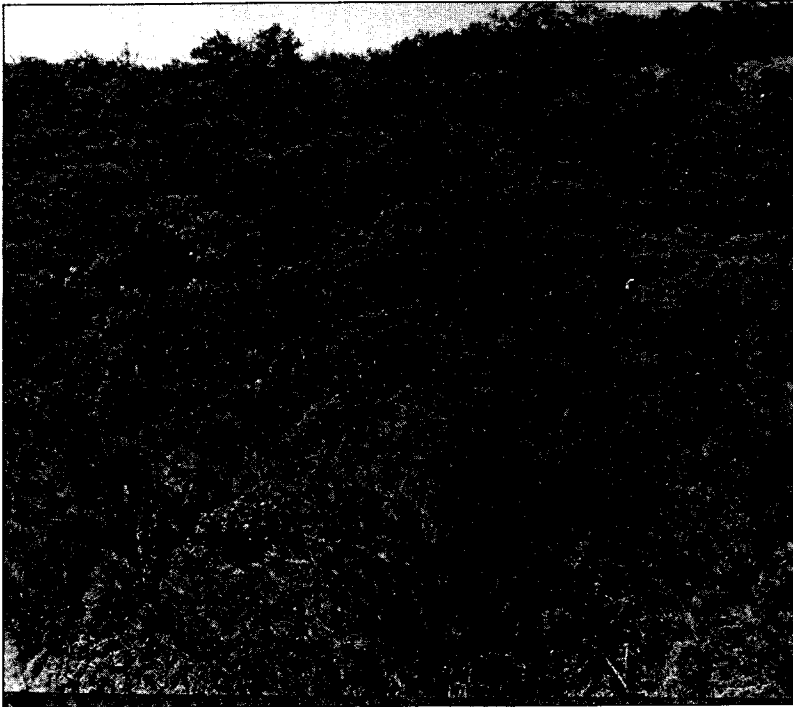


Fig. 1. Chaparral community unburned for over 90 yr in San Diego, County of southern California.

phytotoxic compounds accumulate in older chaparral has, likewise, been challenged (Christensen & Muller 1975; Kaminsky 1981; Keeley & Keeley 1989). Also, several studies have noted significant levels of seedling reproduction in older chaparral (Patric & Hanes 1964; Keeley & Keeley 1988; LLoret & Zedler 1991).

The purpose of this study was to investigate the demographic distribution of living and dead shrubs in stands of chaparral unburned for a half century or longer. Specifically, I wished to examine whether, in the long absence of fires, there are predictable changes in 1) species composition, 2) species diversity, 3) mortality, 4) dispersion of individuals within populations, 5) seedling reproduction and 6) colonization by woodland species.

Study sites

Although fire suppression is often considered an unnatural perturbation of fire-type ecosystems, in the California chaparral the ineffectiveness of fire prevention is possibly of greater importance in dictating fire frequency. As a consequence, human-ignited wildfires are frequent throughout the chaparral type, typically recurring at intervals of 20-30 yr (Keeley 1982). Extensive searching was required to find sites unburned for

more than 50 yr, with the result that the selection of stands largely reflects availability. 12 stands of 0.5 - 1.0 ha, distributed from southern to northern California, were sampled in summer and fall between 1983 and 1985 (Table 1). Stand age was determined from ring counts of non-sprouting shrub species in the stand. Slope aspect was measured with a compass, and slope inclination with an inclinometer. Elevation, latitude, and longitude were taken from USGS 7.5-minute quadrangle topographic maps. Precipitation data were not available for these sites, but the average annual precipitation for the nearest station (NOAA 1984) was adjusted for the difference in elevation using the regression model reported by Miller et al. (1981).

Other than fire, these sites appeared to have had little human caused disturbance, with the single exception of the Sequoia Site. The openness of this site relative to the surrounding vegetation, the dense understory of non-native annual grasses, and human artifacts on the site suggested some clearing had been done at one time.

Methods

At each site 45 2m × 4m plots were selected randomly across the site from coordinates generated by a random number table. Within each plot, the diameter within 10 cm of the ground was measured for all live and

Table 1. Location, elevation, precipitation, slope inclination, slope aspect, stand age, bare ground and woody species diversity for the 12 California chaparral sites, arranged by increasing latitude.

Site	County	Mountain Range	Latitude	Longitude	Elevation (m)	Annual ppt (mm)	Incl. (°)	Aspect	Time since last fire (years)	% bare ground	Species diversity	
											No. of species	*Index
1. San Ignacio	S. Diego	Palomar	33° 17'	116° 37'	1000	625	8	NW	76	18	16	4.67
2. Chihuahua	S. Diego	Palomar	33° 22'	116° 42'	1175	670	17	SE	66	31	7	2.03
3. Silverado	Orange	Santa Ana	33° 45'	117° 33'	950	570	27	NE	118	17	14	6.45
4. Pacific View	Ventura	Santa Monica	34° 05'	118° 58'	375	450	19	W	56	7	17	4.87
5. Serrano	Ventura	Santa Monica	34° 06'	118° 58'	300	430	22	N	56	4	13	2.29
6. Glendora	Los Ang.	San Gabriel	34° 12'	117° 51'	975	600	37	NW	66	7	16	6.37
7. Monte Cristo	Los Ang.	San Gabriel	34° 20'	118° 08'	1000	450	9	E	89	17	6	1.46
8. Mineral King	Tulare	Sierra Nevada	36° 28'	118° 46'	1100	775	14	S	102	7	4	1.49
9. Sequoia	Tulare	Sierra Nevada	36° 28'	118° 46'	1200	800	20	W	83	26	5	2.00
10. Mt. Tamalpais	Marin	North Coast	37° 56'	122° 34'	350	720	24	SE	≥ 93	2	11	4.43
11. Northridge	Marin	North Coast	37° 56'	122° 33'	250	695	24	S	≥ 61	1	9	3.16
12. Bartlett Springs	Lake	North Coast	39° 09'	122° 45'	1075	730	25	SW	74	7	11	5.13

(* Simpson's).

dead woody stems. Seedlings and saplings of woody species were recorded separately from shrubs, and were distinguished by their small stature, distinct taproot, and lack of underground connection with a rootcrown or rhizome of a shrub. Included as seedlings or saplings were any individuals that did not appear to date from the years immediately following the last fire and as such represented 'recent' reproduction. Only in the case of *Rhamnus crocea* were the differences between saplings and adults sometimes indistinct.

Total basal area of live and dead stems was calculated by assuming each stem approximated a circle. Density of stems (ramets) and individual shrubs (genets) was calculated separately for both live and dead stems of adults and seedlings plus saplings. Number of stems per plant was compared within a species between sites and within sites between species with a fixed effect one-way analysis of variance. Pearson product moment correlation was used to evaluate the correlation between densities of live and dead shrubs of each species within plots.

The Simpson Index SI was calculated to give a weighted measure of species richness: $SI = N(N-1) / \sum n(n-1)$, where N = total number of individuals of all species; n = number of individuals of a species. Dispersion was evaluated from the variance/mean ratio of number of individual plants (genets) per plot. A population that is randomly distributed will fit a Poisson distribution, and the variance is equal to the mean. Variance/mean ratios greater than 1 deviate from randomness in the direction of a clumped distribution, and ratios less than 1 deviate towards a regular distribution. A t -test was used to determine whether the observed variance/mean ratio departed significantly from 1 (Cox

1985). To investigate temporal changes in species diversity and dispersion at a site, these statistics were compared for live plants vs live plus dead plants (Kenkel 1988). This is a reasonably robust measure of on-site changes through time because decomposition of shrubs is relatively slow in these semi-arid ecosystems. As an illustration, it was not uncommon to encounter at sites over a century old, charred stems dating back to the last fire. Therefore, it is a reasonable assumption that live plus dead stems is an index of the 'initial' postfire population (excluding, of course, those seedlings and sprouts that died at a very young age).

Additionally, at each site, canopy coverage, shrub height and percentage bare ground were sampled by line intercept along 10 randomly placed 10-m transects. Height was compared between species at the same site with a fixed effect one-way analysis of variance.

12 of the 45 plots sampled for community composition at each site were randomly selected for sampling of the soil and litter. Within a circular plot of 314 cm² (radius = 10 cm), litter depth was measured and all litter was collected. Soil was excavated to a depth of 15 cm or until bare rock was encountered. Litter, defined as organic matter not passing a 2-mm sieve, was separated by flotation, oven-dried to constant mass and weighed. Inorganic matter not passing a 2-mm sieve was separated as rock and weighed. Soil organic matter was determined for three samples from each site by drying the soil to constant mass and determining the percentage mass loss after combustion for one hour at 700 °C (Cox 1985). For half of the sites the variance in organic matter was very high, so a total of six samples were analyzed for these sites. Soil particle-size distribution was determined by a hydrometer as described by Cox

Table 2. Coverage and density of shrubs and seedlings and saplings at the 12 California chaparral sites. Species within a site with the same superscript are not significantly different in number of stems/plant at $P > 0.05$. † = Dead; G = Genet.

	Shrub				Seedling & Sapl.	
	Basal Coverage		Density		Ramets	Density
	m ² /ha	% †	G/ha	% †	per G	(#/ha)
1. San Ignacio						
<i>Quercus dumosa</i> (OR)*	38.23	9.3	1720	0.0	10.5 ^{ab}	8890
<i>Adenostoma fasciculatum</i> (FR)	4.20	32.6	860	32.6	10.3 ^{ab}	0
<i>Ceanothus cuneatus</i> (OS)	2.20	100.0	170	100.0	1.9	0
<i>Rhamnus crocea</i> (OR)	1.97	27.9	420	0.0	9.1 ^{ab}	1330
<i>Adenostoma sparsifolium</i> (OR)	1.67	3.6	200	0.0	3.9	0
<i>Prunus ilicifolia</i> (OR)	0.38	23.7	220	0.0	14.7 ^a	13000
<i>Quercus agrifolia</i> (OR)	0.0	-	0	-	-	1310
Total	50.59	16.0	4960	10.0	-	24610
2. Chihuahua						
<i>Adenostoma fasciculatum</i> (FR)	19.57	11.2	3580	2.2	11.6	0
<i>Ceanothus greggii</i> (OS)	17.68	19.4	750	18.7	2.4	0
<i>Adenostoma sparsifolium</i> (OR)	6.79	5.6	920	3.3	4.7	0
<i>Rhus ovata</i> (OR?)	1.93	20.2	110	0.0	8.5	0
Total	47.05	13.7	5470	4.6	-	0
3. Silverado						
<i>Quercus dumosa</i> (OR)	30.45	8.2	2420	12.8	4.4 ^a	1300
<i>Ceanothus crassifolius</i> (OS)	11.59	68.2	1580	70.3	1.7	0
<i>Heteromeles arbutifolia</i> (OR)	4.84	12.8	310	0.0	17.3	50
<i>Adenostoma fasciculatum</i> (FR)	2.93	46.4	670	37.3	5.0 ^a	0
<i>Cercocarpus betuloides</i> (OR)	1.32	34.1	480	12.5	7.3 ^a	0
<i>Rhamnus crocea</i> (OR)	0.25	8.0	140	0.0	5.4 ^a	920
Total	54.75	25.0	8450	22.7	-	2320
4. Pacific View						
<i>Ceanothus megacarpus</i> (OS)	40.80	12.3	3360	24.7	1.2 ^a	0
<i>Adenostoma fasciculatum</i> (FR)	7.53	35.6	1500	22.0	6.4	0
<i>Salvia mellifera</i> (FR)	6.96	59.3	1920	44.8	3.8 ^a	0
<i>Cercocarpus betuloides</i> (OR)	3.24	20.4	610	0.0	65.8	0
<i>Rhamnus crocea</i> (OR)	1.10	55.5	260	23.1	2.3 ^a	80
Total	66.88	22.2	10940	21.3	-	80
5. Serrano						
<i>Ceanothus spinosus</i> (FR)	47.03	22.7	5830	31.4	6.0 ^a	0
<i>Rhamnus crocea</i> (OR)	2.42	16.1	750	14.7	4.4 ^a	920
<i>Rhamnus californica</i> (OR)	0.16	0.0	220	0.0	1.9	250
Total	51.26	22.6	9160	32.1	-	1170
6. Glendora						
<i>Adenostoma fasciculatum</i> (FR)	11.98	39.1	1940	50.0	4.7 ^a	0
<i>Quercus dumosa</i> (OR)	9.61	7.0	860	0.0	7.6 ^a	80
<i>Garrya veatchii</i> (OR?)	8.34	21.9	420	7.1	8.5 ^a	0
<i>Heteromeles arbutifolia</i> (OR)	5.64	12.9	330	0.0	30.5 ^b	0
<i>Arctostaphylos glauca</i> (OS)	3.71	23.7	220	13.6	1.8 ^c	0
<i>Ceanothus crassifolius</i> (OS)	3.54	34.7	750	77.3	1.7 ^c	0
<i>Prunus ilicifolia</i> (OR)	3.49	35.2	310	9.7	29.6 ^b	4530
Total	48.61	24.2	5400	31.5	-	4640
7. Monte Cristo						
<i>Arctostaphylos glauca</i> (OS)	50.10	16.6	2440	19.3	4.4 ^a	0
<i>Ceanothus crassifolius</i> (OS)	33.96	59.1	3810	82.4	2.1 ^a	0
<i>Adenostoma fasciculatum</i> (FR)	31.39	35.2	6690	32.7	5.5 ^a	0
<i>Quercus dumosa</i> (OR)	2.42	1.2	220	0.0	5.9 ^a	0
Total	117.96	33.5	13280	43.8	-	30
8. Mineral King						
<i>Arctostaphylos viscida</i> (OS)	51.82	9.0	1220	11.5	2.2	0
<i>Adenostoma fasciculatum</i> (FR)	53.19	35.8	5780	22.7	7.8	0
Total	105.39	22.7	7060	20.5	-	0

	Shrub				Seedling & Sapl.	
	Basal Coverage		Density		Ramets	Density
	m ² /ha	% †	G/ha	% †	per G	(#/ha)

9. Sequoia						
<i>Ceanothus cuneatus</i> (OS)	33.84	31.5	1140	5.3	4.2 ^a	30
<i>Cercocarpus betuloides</i> (OR)	13.92	20.8	670	4.5	23.2	36530
<i>Rhamnus crocea</i> (OR)	0.68	51.5	30	0.0	4.0 ^a	690
Total	48.67	29.0	1860	4.3	-	37580

10. Mt. Tamalpais						
<i>Quercus wislizenii</i> (OR)	20.18	6.6	2600	1.9	4.1 ^a	26980
<i>Arctostaphylos glandul.</i> (FR)	20.96	23.9	3100	33.9	4.8 ^a	125
<i>Heteromeles arbutifolia</i> (OR)	2.63	18.6	750	33.3	13.3	800
Total	44.76	15.6	12960	13.3	-	28530

11. Northridge						
<i>Arctostaphylos glandul.</i> (FR)	28.53	18.8	13870	18.9	3.3 ^a	0
<i>Quercus wislizenii</i> (OR)	11.89	0.0	500	0.0	5.0 ^a	0
<i>Adenostoma fasciculatum</i> (FR)	10.00	13.5	9030	16.9	2.6 ^a	0
<i>Heteromeles arbutifolia</i> (OR)	3.13	7.7	1400	0.0	15.1	0
Total	55.32	12.7	29500	14.5	-	0

12. Bartlett Springs						
<i>Arctostaphylos elegans</i> (OS)	16.00	1.4	380	0.0	3.4 ^a	0
<i>Ceanothus cuneatus</i> (OS)	13.75	29.3	980	38.8	2.1 ^a	0
<i>Garrya flavescens</i> (OR?)	11.79	21.5	1900	0.0	8.1 ^b	0
<i>Quercus dumosa</i> (OR)	10.27	4.4	1410	0.0	16.5 ^c	1300
<i>Cercocarpus betuloides</i> (OR)	8.47	17.5	820	0.0	17.5 ^c	50
<i>Adenostoma fasciculatum</i> (FR)	5.96	30.0	2180	27.5	5.8 ^{ab}	0
Total	67.64	15.5	7880	12.4	-	1520

* = Postfire reproductive mode; OR = obligate resprouter; FR = facultative resprouter; OS = obligate seeder.

(1985) for three soil samples from each site. Soil pH was measured on three samples incubated overnight in 1:1 (m/v) soil/distilled water.

Ages were determined from ring counts made on all stems on five shrubs of the dominant species at each site. All stems were cut at 5 - 10 cm aboveground and a several cm-thick section was returned to the lab. Stem sections were sanded (200-300 grit) and growth rings counted under a dissecting scope at 7-10 × power by two independent observers. Use of counts to determine the age of woody stems not only requires the presence of distinct growth rings, but also verification that they represent annual rings. Ring counts on stems from stands of known age, plus synchrony in annual growth ring width among species in the same stand, were taken as evidence that growth rings represented annual rings (Keeley unpubl. data).

Results

The 12 stands varied widely in species dominance (Table 2). *Adenostoma fasciculatum* was present in all but two of the sites, and the next most frequent species was *Rhamnus crocea* ssp. *ilicifolia*, present at all but four of the sites. Total canopy coverage ranged from 79% to 100% (not including overlapping branches).

Some stands had nearly a closed canopy throughout, while others had many large gaps as indicated by a large percentage of bare ground (Table 1).

Total live plus dead basal area coverage was generally between 50-60 m² ha⁻¹, except for sites dominated by non-sprouting *Arctostaphylos* species (Table 2); these shrubs produced exceptionally massive trunks. The percentage of dead basal area ranged from 13% to 34% and was not correlated with stand age ($r = 0.40$, $P > 0.05$, e.g. the two oldest stands had 23-25% and the two youngest stands 22-23%), or with any other stand parameter (data not shown). Non-sprouting species (postfire obligate seeders) were divergent in extent of mortality in these older stands. *Ceanothus* species accounted for much of the dead, whereas non-sprouting *Arctostaphylos* species had relatively little dead basal coverage (Table 2). Stands with a high percentage of dead *Ceanothus* were those dominated by species such as *Quercus dumosa*, which had over-topped the *Ceanothus* (Table 3). Mortality of *Ceanothus* was significantly correlated with stand age and contrasts markedly with the general lack of mortality in *Quercus* (Fig. 2). Older sites also tended to have relatively high *Adenostoma* mortality.

A correlation analysis of the number of living shrubs per plot vs. number of dead for all species combinations at a site produced the following significant correlations ($P < 0.01$). Live *Quercus* were correlated with dead *Ceanothus* at Silverado ($r = 0.36$) and Bartlett Springs ($r = 0.46$). Live *Adenostoma* were correlated with dead *Adenostoma* at Monte Cristo ($r = 0.33$) and at Mineral King ($r = 0.41$). At Pacific View live *Ceanothus* were correlated with dead *Adenostoma* ($r = 0.31$).

Shrub density varied by more than 10-fold among

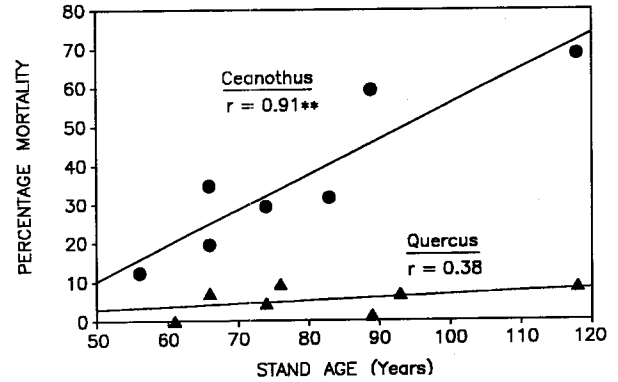


Fig. 2. Mortality of non-sprouting *Ceanothus* spp. and sprouting *Quercus* spp. in stands of different ages. ** = $P < 0.01$.

sites, but stem (ramet) density was less variable (Table 2). Number of ramets per genet was also variable between species and between sites, ranging from 1 to more than 100 (Table 2). The non-sprouting species of *Ceanothus* and *Arctostaphylos* were commonly single-stemmed, whereas some resprouting species such as *Heteromeles arbutifolia* had a proliferation of basal sprouts. Three species had statistically significant differences ($P < 0.05$) in number of stems per plant between sites. *Adenostoma fasciculatum* had more stems per plant at the two southern most sites than all other sites. *Quercus dumosa*, on the other hand, had significantly more stems at the most northern population than at other sites.

Origin of sprouts varied among species and sites. In most cases sprouts initiated at the base of the stem or root crown, but *Quercus dumosa* and *Cercocarpus betu-*

Table 3. Shrub and seedling height for dominant species. Species within a site with the same superscript are not significantly different at $P > 0.05$.

Site:	Height (m)											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Adenostoma fasciculatum</i>	2.5 ^a	2.1 ^a	-	3.3 ^a	-	2.3 ^a	1.9 ^a	1.7	-	-	1.5 ^a	1.7 ^a
<i>Arctostaphylos</i> spp.	-	-	-	-	-	2.0 ^a	3.2 ^b	2.8	-	2.8 ^a	1.5 ^a	-
<i>Ceanothus</i> spp.	2.0 ^a	2.0 ^a	2.1 ^a	2.9 ^a	4.2	-	3.3 ^b	-	2.0	-	-	2.0 ^a
<i>Cercocarpus betuloides</i>												
Adults	-	-	1.6 ^a	1.9	-	-	-	-	4.2	-	-	2.5 ^a
Seedl./sapl.	-	-	-	-	-	-	-	-	1.1	-	-	-
<i>Heteromeles arbutifolia</i>	-	-	2.5 ^{a,b}	-	-	4.1 ^b	-	-	-	2.2 ^a	1.3 ^a	-
<i>Prunus ilicifolia</i>												
Adults	-	-	-	-	-	1.5 ^a	-	-	-	-	-	-
Seedl./sapl.	0.2	-	-	-	-	0.3	-	-	-	-	-	-
<i>Rhamnus crocea</i>												
Adults	2.8 ^{a,b}	-	-	2.5 ^a	2.1	-	-	-	-	-	-	-
Seedl./sapl.	0.4	-	0.3	-	-	-	-	-	-	-	-	-
<i>Quercus</i> spp.												
Adults	3.5 ^b	-	3.5 ^b	-	-	3.6 ^b	-	-	-	2.9 ^a	-	2.3 ^a
Seedl./sapl.	0.1	-	0.1	-	-	-	-	-	-	0.2	-	0.2

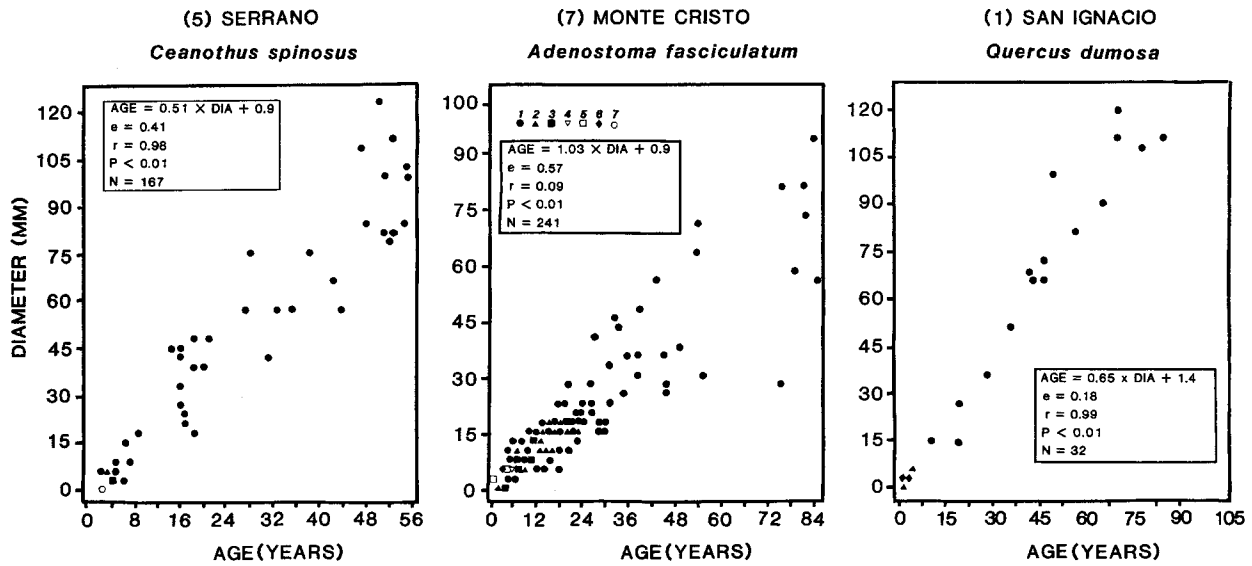


Fig. 3. Bivariate plot of stem age and diameter for all stems on five shrubs of three resprouting species. Symbols indicate more than one observation; r = correlation coefficient, e = standard error of mean.

loides also produced sprouts from roots, often a meter or more from the main trunk. The latter species had a profusion of these root and rhizome sprouts at the Pacific View Site, where the adult plants were largely overtopped by other shrub species (Table 3). At sites such as Sequoia, where *S. betuloides* dominated, all sprouts came from the stem base.

Shrub stem density at a site was significantly correlated with latitude ($r = 0.59$, $P < 0.05$), longitude ($r = 0.97$, $P < 0.01$), and soil organic matter ($r = 0.68$, $P <$

0.05), and negatively correlated with age ($r = -0.61$, $P < 0.05$), percentage bareground ($r = -0.65$, $P < 0.05$), dead basal area ($r = -0.55$, $P < 0.05$), and soil pH ($r = -0.73$, $P < 0.05$). Multi-stemmed shrubs produced shoots varying in diameter from 1 mm to more than 100 mm, and all resprouting species showed a significant correlation between age and size. The age distribution of stems on three multi-stemmed shrub species illustrates that recruitment occurred throughout the period between fires (Fig. 3). All multi-stemmed resprouting

Table 4. Dispersion as measured by the variance/mean ratio for shrubs and seedlings and saplings of woody plants in plots at the 12 chaparral sites. Populations are randomly distributed unless starred; * = variance/mean ratio significantly different from 1.0 at $P < 0.05$, ** = $P < 0.01$.

Site:	Variance / Mean											
	1	2	3	4	5	6	7	8	9	10	11	12
<i>Adenostoma fasciculatum</i>	2.2*	4.5**	1.4	2.3**	-	3.5**	2.3**	2.2**	-	-	2.4**	1.8**
<i>Arctostaphylos</i> spp.	-	-	-	-	-	0.8	1.1	1.2	-	1.6	1.6	-
<i>Ceanothus</i> spp.	-	1.0	2.9**	1.8**	1.6**	1.2	1.2	-	1.3	-	-	1.4
<i>Cercocarpus betuloides</i>	-	-	-	0.6	-	-	-	-	0.8	-	-	1.9**
Adults	-	-	-	-	-	-	-	-	-	-	-	-
Seedl./sapl.	-	-	-	-	-	-	-	-	142.9**	-	-	-
<i>Heteromeles arbutifolia</i>	-	-	0.9	-	-	1.9**	-	-	-	3.3**	2.8*	-
Adults	-	-	-	-	-	-	-	-	-	-	-	-
Seedl./sapl.	-	-	-	-	-	-	-	-	-	2.5**	-	-
<i>Prunus ilicifolia</i>	-	-	-	-	-	2.2**	-	-	-	-	-	-
Adults	-	-	-	-	-	-	-	-	-	-	-	-
Seedl./sapl.	28.4**	-	-	-	-	9.7**	-	-	-	-	-	-
<i>Rhamnus crocea</i>	-	-	-	-	1.8**	-	-	-	0.8	-	-	-
Adults	1.2	-	-	-	1.6**	-	-	-	18.1**	-	-	-
Seedl./sapl.	1.9**	-	6.2**	-	-	-	-	-	-	-	-	-
<i>Quercus</i> spp.	-	-	-	-	-	-	-	-	-	-	-	-
Adults	1.1	-	1.4*	-	-	2.0**	-	-	-	1.2	1.4	1.6
Seedl./sapl.	43.8**	-	5.6**	-	-	-	-	-	-	10.8**	-	3.5**

shrubs had a range of stem ages on the same shrub. In contrast, the age of all single stemmed, non-sprouting *Ceanothus* and *Arctostaphylos* shrubs always dated back to the last fire.

Species richness ranged from 4 - 17 woody taxa at a site and there was a several-fold difference in Simpson's Index of species diversity between sites (Table 1). Species diversity was not correlated with stand age ($r = 0.02, P > 0.05$); the oldest stand had the highest diversity and the next oldest stand had the lowest (Table 1), but diversity was correlated with slope inclination ($r = 0.72, P < 0.05$). Comparison of live with live plus dead (initial population) showed little change in diversity due to mortality. At half of the sites there was no decrease in Simpson's Index of species diversity when live plants were compared to live plus dead (data not shown), and for the other sites there was < 8% decrease in the species diversity index.

Many shrub populations were spatially clumped as indicated by a variance/mean ratio significantly greater than 1 (Table 4). The variance/mean ratio for live plus dead plants, compared to live plants alone, indicated that, as populations thinned, they progressed to a less clumped distribution. For non-sprouting species of *Ceanothus*, which suffered extensive mortality at some sites, this pattern was particularly evident (Fig. 4). *Arctostaphylos* taxa were unique in that they were always randomly distributed.

Large seedling and sapling populations were present at seven of the sites (Table 2). Significant recruitment, ranging from 1000 to 36 500 ha⁻¹, was found for *Quercus dumosa*, *Q. wislizenii*, *Rhamnus crocea*, *Prunus ilicifolia*, *Heteromeles arbutifolia* and *Cercocarpus betuloides*. Considerable seedling and sapling establishment was observed at several sites for *Quercus dumosa* and *Rhamnus crocea*. *Heteromeles arbutifolia* and *Cercocarpus betuloides* shrubs were present at several sites but seedlings were abundant at only a single site for each species. Significant seedling populations were never observed for species of *Adenostoma*, *Arctostaphylos*, *Ceanothus*, *Garrya* or *Rhus*.

Significant seedling establishment was present at one or more sites in each of the four mountain ranges investigated. In southern California these sites tended to be on north-facing slopes, but other slopes were represented. Seedling and sapling establishment was significantly correlated with species diversity ($r = 0.71, P < 0.05$), litter depth ($r = 0.76, P < 0.01$) and biomass ($r = 0.57, P < 0.05$). In general, stands with significant recruitment were composed of shrubs of the same species as the seedlings and saplings (Table 2). Sites dominated by non-seedling producing taxa such as *Adenostoma*, *Arctostaphylos* and *Ceanothus*, were not invaded by seedlings of other species.

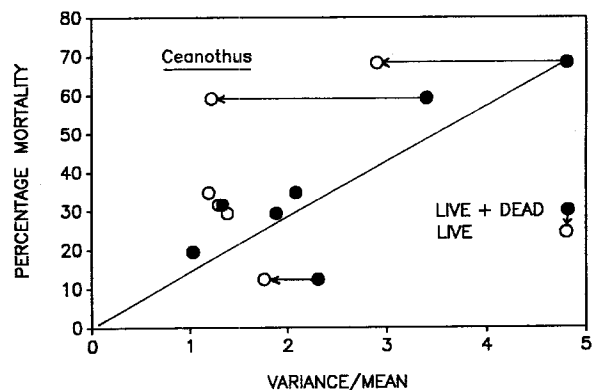


Fig. 4. Dispersion of *Ceanothus* taxa in stands of differing age. Regression line for live plus dead (filled circles; $r = 0.83, P < 0.05$). Arrows indicate change in variance/mean for the same population resulting from mortality.

Colonization by woodland elements was observed at several sites. At the San Ignacio Site *Quercus agrifolia*, a tree typical of oak woodlands and not present at the site (the nearest seed source was within 50 m), had a significant seedling population (Table 2). Another woodland species, *Umbellularia californica*, had a low density (#/ha) of seedlings colonizing Glendora (28), Sequoia (83), Mt. Tamalpais (325) and Northridge (150). *Arbutus menziesii* seedlings were present at Mt. Tamalpais (50) and *Aesculus californica* and *Pinus sabiniana* seedlings were present at Bartlett Springs (50 and 54, respectively).

Some species had seedlings and saplings with multiple stems initiated from a swollen base or tuber; they were *Prunus ilicifolia* at San Ignacio ($\bar{X} = 2.0 \pm \text{S.D.} = 2.9, N = 163$), *Quercus dumosa* at Silverado ($1.4 \pm 0.8, 146$) and *Q. wislizenii* at Mt. Tamalpais ($1.9 \pm 2.2, 434$). Observations of remnant stems severed near the base suggested that animal grazing was responsible for loss of the main shoot.

Although average height of seedlings and saplings did not vary greatly among sites (Table 3), the variance within a site was sometimes high due to inclusion of saplings of various ages. For example, at San Ignacio *Quercus dumosa*, *Prunus ilicifolia* and *Rhamnus crocea* had one to several saplings exceeding 2.0 m in height, although all had rather spindly stems between 2 to 3 cm diameter. For these three species, height was significantly correlated ($P < 0.01$) with age; $r = 0.65$ ($n = 323$), 0.86 ($n = 468$) and 0.89 ($n = 48$), respectively. At the Silverado Site none of the species had saplings exceeding 1.5 m height, though height and age were significantly correlated and this was true for species at other sites as well. Occasionally saplings were quite stunted;

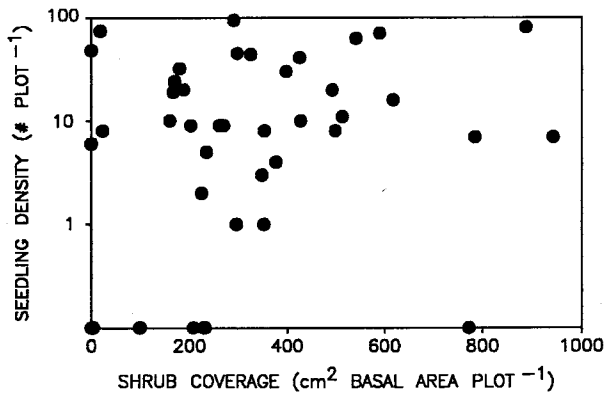


Fig. 5. Distribution of seedlings relative to shrub cover at the San Ignacio. Because several plots lacked seedlings, log density + 0.1 is plotted ($r = 0.08$, $N = 45$).

e.g. at Silverado the oldest *Quercus dumosa* sapling was 34 yrs but it was less than 1 m tall and the stem diameter was 2 cm.

In most cases seedlings were distributed in a highly clumped fashion, as evidenced by very high variance/mean ratios (Table 4). Seedlings at all sites except the disturbed Sequoia Site were distributed under the shrub canopy and were seldom found in gaps; there was no significant relationship between shrub coverage and seedling and sapling recruitment, and this is illustrated for seedlings and saplings at the San Ignacio Site (Fig. 5).

Sub-shrub or liana species (e.g. *Lonicera subspicata*, *Penstemon cordifolius*, *Mimulus longifolius*, *M. aurantiacus*, *Rhus diversiloba*, *Ribes californicum* and *Symphoricarpus mollis*) were present largely from recent reproduction, although great age was suggested for the lianas *Lonicera subspicata* and *Rhus diversiloba* by the stems which occasionally exceeded 100 mm diameter. Presence or absence of these subordinate species was largely responsible for differences in species diversity among sites.

Discussion

Century old chaparral is dominated by vigorous shrub populations, not obviously senile or senescent, and there is no evidence of a decline in number of species with age; the richest community in this study was 118 yr of age (Table 1). With the exception of immediately after fire, older stands (see also Hedrick 1951; Patric & Hanes 1964) are not less diverse than much younger chaparral (Horton & Kraebel 1955; Specht 1969; Hanes 1971; Davis, Hickson, & Odion 1988). Some very ancient stands were depauperate in species,

but examination of the dead shrubs in the stands revealed that these sites were also depauperate when they were much younger (Table 2).

Based on live to dead ratios (Table 2), it is clear that species differ in their longevity. Sprouting shrubs generally seem to have great longevity. In particular, *Quercus* shrubs suffer relatively little mortality in older stands (Table 2, Fig. 2). Indeed, at the 118 yr old Silverado Site, this taxon had an abundance of new growth and appeared to be quite vigorous. In contrast, non-sprouting *Ceanothus* species had extensive mortality in some, but not all, stands (Fig. 2). Generally, *Ceanothus* spp. suffered the most in close competition with other shrubs which were able to overtop them, such as *Quercus* and *Heteromeles* (Table 3). However, when these taxa were not present, mortality of *Ceanothus* was relatively slight (e.g., Chihuahua and Pacific View; Table 2). Predictions based on the age-structure of dead stems at Pacific View are that this site will be dominated by *C. megacarpus* for many years to come (Montygiard-Loyba & Keeley 1986). In general, non-sprouting *Ceanothus* seem to succumb to competition with other species, in particular *Quercus* and *Heteromeles*, but on more open, usually arid sites, *Ceanothus* are capable of great longevity (see also Keeley 1975).

A commonly accepted paradigm is that shrub mortality in older chaparral stands reflects an inherently short lifespan, and death is the culmination of a general senescence process. I suggest senescence is not an adequate explanation because taxa such as *Ceanothus*, which suffer the greatest mortality in older stands (Table 2, Fig. 2), are not in a state of physiological decline (Reid 1985), nor are they in a post-reproductive state, which is normally considered a characteristic of senescence (Gatsuk et al. 1980). One characteristic of these non-sprouting *Ceanothus*, which leads to the conclusion of senescence, is the occasional observation of mass mortality within a stand. In general, this occurs in severe drought years (Keeley pers. obs. in 1976, 1981, 1987, 1990) and is likely due to the shallow root systems that expose these species to extremely low xylem water potentials during summer drought (Schlesinger et al. 1982).

An alternative to the model of stand senescence is one of a shifting balance in the competitive relationships as the community ages, resulting in successional replacement of one population by another (sensu Peet & Christensen 1980). In brief, non-sprouting *Ceanothus* are adapted for rapid growth after fire, but at a cost of being poor competitors later in succession. Much of this 'cost' may derive from the fact that these shrubs develop from seed. Consequently, at any stage of post-fire development *Ceanothus* has lower root-to-shoot ratios than species such as *Quercus*, which regenerate from

massive rootcrowns (Kummerow & Mangan 1981). The consequence of this morphological difference is that *Ceanothus* experiences substantially lower xylem water potentials during the summer drought than does *Quercus* (Poole, Roberts, & Miller 1981; Davis 1989). Studies have shown that that water stress may be lethal for *Ceanothus* on some sites in certain years (Schlesinger et al. 1982; Davis 1989). In addition, the rapid postfire regrowth typical of *Ceanothus* requires adaptation to high light environments, and consequently such taxa are poor competitors in low light environments (Oechel & Lawrence 1979; Schlesinger et al. 1982; Mahall & Wilson 1986). In particular, under shaded conditions *Ceanothus* has reduced water use efficiency which puts it at greater risk to lethal water stress conditions. Consequently, as a stand ages an increasing proportion of the biomass is in stems with the consequence that the proportion of photosynthetic biomass decreases and the respiratory demand by woody tissue increases.

Quercus are more shade tolerant than *Ceanothus*, and their massive root systems are capable of maintaining substantially higher xylem water potentials during the summer drought and, thus, are rarely stressed to lethal levels (Miller & Poole 1979; Oechel et al. 1981; Davis 1989). *Quercus* are capable of sustaining growth through the summer drought, and as a consequence total seasonal carbon gain is substantially greater for *Quercus* than for *Ceanothus* (Oechel et al. 1981). In mixed stands, *Quercus* often overtops (Table 3) and suppresses the *Ceanothus*. If *Ceanothus* is able to remain above the *Quercus*, it is only by increasing the proportion of carbon to stem growth, in which case it may eventually accumulate aboveground biomass in excess of what the roots can support with water and nutrients. Once established, *Quercus* is nearly immortal due to the continuous establishment of new shoots (Fig. 3).

There is indirect evidence linking competition to mortality of *Ceanothus*. Schlesinger et al. (1982) showed that intraspecific competition was the driving force behind thinning of young stands of *Ceanothus*. They suggested that competition was reflected in the non-random mortality during stand thinning which was greatest in localized high-density clumps and decreased with distance to nearest neighbor. They maintain that competition for water is an important component of mortality; smaller shrubs suffer greater summer water stress and are the most likely to succumb during intra-specific thinning.

This pattern of thinning is also evident in older stands where it is observed that mortality is a function of the pattern of dispersion (Fig. 4). Sites where *Ceanothus* were highly clumped early in succession (high variance to mean ratio for live and dead shrubs)

were sites where mortality was greatest. On these sites mortality resulted in a marked reduction in the variance/mean ratio for surviving shrubs (Fig. 4).

Not all non-sprouting taxa succumb readily to competition. *Arctostaphylos* species seem to be particularly long lived (e.g. Monte Cristo and Mineral King Sites, Table 2). Such species are quite vigorous in older stands and capable of substantial annual production (Keeley & Keeley 1977). Like *Ceanothus*, these taxa are also shallow rooted, but they are capable of arborescent proportions (Table 3) and, thus, they remain above competing vegetation.

Adenostoma fasciculatum is a sprouting species that shares the requirement for open sites typical of non-sprouting *Ceanothus*. *Adenostoma* is capable of great longevity on open sites such as Chihuahua or Mineral King where vigorous populations over 100 yrs of age were observed (Table 2). In close competition with shrubs such as *Quercus dumosa*, *Adenostoma* is readily over-topped (Table 3) and suffers much mortality (Table 2). There is a physiological basis for this in that photosynthesis and water use efficiency are greatly inhibited when shaded (Miller & Stoner 1979).

Seedling regeneration

Seedling establishment in chaparral follows two patterns. Shrubs such as *Adenostoma fasciculatum*, *Arctostaphylos* spp. and *Ceanothus* spp. have seedling recruitment restricted to the first season after fire. This characteristic has earned these shrubs the label of fire-dependent or 'fire-recruiter' species (Keeley 1991).

Many other shrubs are not fire-recruiters and persist after fires solely by vegetative regeneration. I suggest 'fire-persister' species would be a coordinate term for shrubs such as *Quercus* spp., *Rhamnus* spp., *Heteromeles arbutifolia*, *Cercocarpus betuloides*, and *Prunus ilicifolia*. The conditions necessary for successful seedling establishment by these fire-persister shrubs are not well understood. Although all are capable of substantial seed production soon after fire, seedlings are seldom observed in mature chaparral stands of < 50 yrs of age. With few exceptions, reports of successful seedling establishment in unburned chaparral have been from much older stands (Patric & Hanes 1964; Zedler 1981; Parker & Kelly 1989; Lloret & Zedler 1991).

Discerning the factors responsible for seedling recruitment in the absence of fire requires careful analysis. All of these species are physiological 'drought avoiders' (sensu Mooney & Miller 1985). Since these species resprout after fire, well established plants have massive root systems that penetrate rock fractures and maintain relatively high xylem water potentials during the summer drought. Based on xylem characteristics,

these shrubs are described as having a high mesomorphy ratio (Carlquist & Hoekmann 1985), which likely contributes to their inability to withstand low water potentials; these shrubs will succumb at xylem water potentials markedly higher than is lethal for postfire seeders such as *Ceanothus*, *Adenostoma* or *Arctostaphylos* (Oechel et al. 1981; Davis 1989). As a consequence, seedlings of *Quercus*, *Rhamnus*, *Rhus* and *Prunus* are particularly vulnerable to soil drought. Thus, safe sites for these taxa are shaded areas beneath the shrub canopy with a dense layer of moisture retaining litter. The extremely clumped distribution of seedlings beneath the shrub canopy suggests that suitable conditions for establishment are not evenly distributed throughout the site. Restriction of reproduction to ancient stands may reflect the need for long fire-free periods to develop a litter layer sufficient to support seedling survival.

Despite significant levels of reproduction, there was little evidence that saplings successfully reached the canopy in any stand. The tallest saplings observed were still > 1 meter below the mature shrubs and most were much smaller. Herbivory was observed to be an important factor keeping the saplings stunted, and this has also been documented for *Quercus durata* from northern California (Williams et al. in press). It was observed in the present study that many of the *Quercus* and *Prunus* seedlings that had been repeatedly clipped by herbivores, produced a coppice growth and enlarged basal burl. Such a burl may play a prominent role in allowing these seedlings to resprout successfully after fire. It would be under these conditions that resprouting saplings may find their greatest opportunity for recruitment into the adult population.

Conclusions

Chaparral unburned for a century or more remains a viable community of vigorous shrubs with little evidence of a decline in species diversity or successional replacement by other vegetation types. In the long-term absence of fire, mesic closed communities of chaparral are dominated by fire-persister shrubs (*Quercus*, *Rhamnus*, *Prunus*, *Heteromeles*) at the expense of fire-recruiter shrubs. The success of one group over the other varies across the landscape. On arid, open sites fire-persister species do poorly and fire-recruiters (*Adenostoma*, *Arctostaphylos*, *Ceanothus*) dominate. Temporal variation in success may also play a role in the coexistence of these two strategies. Opportunities for population expansion increase after fire for the latter species, but for fire-persisters, opportunities for population expansion increase only with long-term absence of fire.

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