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Post-Fire Regeneration Strategies of Californian Coastal Sage Shrubs

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Summary. Regeneration methods of coastal sage scrub vegetation after fire were studied in the coastal Santa Monica Mountains of southern California. Six sites were sampled two years after a large fire of fall, 1978. The intensity of fire varied. Foliar cover and flowering incidence were recorded for individuals regenerating by resprouting or from seed. Resprouting plants contributed most to post-fire recovery, comprising 95% of the relative foliar shrub cover; 84% of resprout and 47% of seedling cover had flowered. An ANOVA of reproductive mode and fire intensity indicates that resprout total cover and individual size are significantly greater than those of seedlings, regardless of fire intensity. Among sites the average foliar cover of resprouts exceeded that of seedlings by factors ranging from 9 to 63. All coastal sage species examined resprout, although the potential vigor of resprouting appears to vary widely within genera (e.g. *Encelia, Eriogonum*, and *Salvia*) and even within species. In the second growing season following fire seedling density increased due to seeds shed by resprouted shrubs. Most of the cover on these stands of coastal sage scrub is destined to be either crown-sprouted individuals or their progeny.

Californian coastal sage scrub is a predominantly semi-deciduous, sub-ligneous shrubland in the Mediterranean climate zone of California. A number of authors have reported different observations regarding the ability of dominant species to resprout from root crowns following fire. Some authors (Horton and Kraebel 1955; Hanes 1971; Zedler 1977; Kirkpatrick and Hutchinson 1980) reported only sporadic resprouting ability among sage species. On the other hand Wells (1962), Westman (1981 a), and Westman et al. (1981) reported widespread resprouting ability among sage dominants; the latter authors noted, however, that the extent of sprouting following a particular fire is variable.

In chaparral Keeley (1977) noted that the most abundant species, *Adenostema fasciculatum*, reproduces both by resprouting and seeding. The same is true for most coastal sage dominants. In this paper we quantify the contributions to post-fire recovery of the resprouting vs. seeding strategies of coastal sage shrubs in the coastal Santa Monica Mountains, Los Angeles County, California, USA.

Methods

Study Area

We chose six sites in the coastal Santa Monica Mountains between Point Dume and Sequit Point. Sites 1 and 2 are on south and north-facing slopes with andesite and sandstone substrates respectively. Sites 3 and 4 are on east-facing slopes of arkose sandstone and sites 5 and 6 are on west-facing slopes of interbedded sandstone and shale. All sites burned in a single large fire of October 23–24, 1978 which covered 10,000 ha. Sites 1–4 burned in early afternoon under low humidity and high winds. Sites 5 and 6 burned in a cooler backfire at about 2 a.m.

Samples

The sample sites were 24 × 24 m and were surrounded by similar vegetation. Four 2 × 2 m quadrats were randomly placed along each of four randomly placed parallel transects. In each quadrat we determined the number of individuals of each shrub species which had resprouted from root crown or regenerated from seed. In order to be considered a resprout the root crown had to be charred. Thus we may have misclassified some resprouts as seedlings. We measured canopy diameter, or length and width for irregularly shaped canopies, to determine shrub cover. The canopies of all shrubs in the quadrat were measured; only plants whose stem bases were in the quadrat were counted for density samples.

Analysis

Plant size, density, and cover values were normalized by logarithmic transformation and subjected to analysis of variance (ANOVA, Dixon and Brown 1979). We tested the three variables in a 2-way ANOVA by reproductive mode (sprout or seedling) and fire intensity (afternoon or night fire, sites 1–4 and 5–6). We also examined the variability of reproductive mode in the nine most frequent species and in the remaining eight species (Table 1).

Results

Resprouting plants made the greatest contribution to foliar cover following fire. Resprouts contribute 94.7% relative foliar shrub cover (79.3% from flowering individuals). Seedling cover was only 5.3% (2.8% from flowering indi-

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Table 1. Percent foliar cover of shrubs found on sample sites. Values without parentheses represent total relative cover of species, and those within are cover of flowering shrubs only

Species	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6	
	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling
Artemisia californica	3.2	0.3	0.1	*	0.6	0.1	0.1	*	0.5	0.1	1.3	0.4
	(3.2)	(0.1)	(0.1)	–	(0.6)	–	(0.1)	–	(0.5)	(*)	(1.3)	(0.3)
Encelia californica	2.1	0.3	–	–	8.9	1.6	1.9	–	11.9	0.5	5.2	1.2
	(2.1)	–	–	–	(8.9)	(1.3)	(1.9)	–	(11.9)	(0.5)	(5.2)	(1.1)
Eriogonum cinereum	2.2	*	14.4	*	6.7	0.1	2.1	*	23.4	0.2	11.8	0.1
	(2.2)	(*)	(14.2)	–	(6.7)	–	(2.1)	–	(23.3)	(*)	(11.4)	(0.1)
Haplopappus squarrossus	5.3	1.7	33.8	2.2	–	–	6.5	1.5	–	–	–	–
	(5.3)	(1.5)	(32.9)	(1.2)	–	–	(6.4)	(1.1)	–	–	–	–
Rhamnus crocea	*	–	–	–	–	–	–	–	–	–	0.9	–
	–	–	–	–	–	–	–	–	–	–	–	–
Rhus laurina	9.1	*	–	–	7.2	*	8.9	*	–	–	3.2	*
	(4.7)	–	–	–	(7.2)	–	(8.9)	–	–	–	(3.2)	–
Salvia leucophylla	*	–	8.8	*	–	–	–	–	4.8	*	7.8	0.1
	(*)	–	(8.4)	–	–	–	–	–	(1.2)	–	(7.4)	–
Salvia mellifera	4.6	0.7	–	–	5.4	2.8	15.3	0.7	0.1	–	–	–
	(4.6)	(0.3)	–	–	(5.4)	(0.3)	(14.3)	–	(0.1)	–	–	–
Yucca whipplei	4.3	*	–	–	12.1	0.1	8.8	*	4.3	–	10.8	*
	(2.2)	–	–	–	(2.5)	–	(3.6)	–	–	–	(4.6)	–

* = cover < 0.05, — = not present
Species found on only one site: *Ceanothus megacarpus, Heteromeles arbutifolia, Isomeris arboreus, Malacothamnus fasciculatus, Mimulus longiflorus, Opuntia littoralis, Rhus integrifolia, Rhus ovata*

Table 2. Extrapolated density of individuals/ha and mean size (cm^2)

Species	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6	
	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling	re-sprout	seed-ling
Artemisia californica	3437	7500	312	156	312	312	312	56719	781	469	625	6250
	941.5	38.9	425	1	275	27.5	1815	1	646	108.3	2080	61.8
Encelia californica	1406	469	–	–	1560	–	2187	2812	1875	1094	1406	2812
	1473.2	70	–	–	1227	–	4088.8	569.9	6330.5	443.6	3660	408.4
Eriogonum cinereum	2656	6719	12031	3750	2031	2344	1250	72187	5312	19531	4062	13437
	843.6	6.4	1192	1.2	1047.7	4.1	5326.9	1	4400	8.7	2902	8.2
Haplopappus squarrossus	7500	10312	19375	45000	4531	6094	–	–	–	–	–	–
	700.1	163	1746	49.7	1429.8	241.4	–	–	–	–	–	–
Rhamnus crocea	312	–	–	–	–	–	–	–	–	–	312	–
	1505	–	–	–	–	–	–	–	–	–	2975	–
Rhus laurina	469	625	–	–	612	156	156	625	–	–	156	156
	19391.7	32	–	–	28500	15	46100	33.1	–	–	20600	100
Salvia leucophylla	156	–	5625	156	–	–	–	–	2031	612	4687	625
	37	–	1561	200	–	–	–	–	2381.9	16.5	1670.5	85
Salvia mellifera	1719	9844	–	–	9219	22969	1406	8750	156	–	–	–
	2674.3	73.5	–	–	1655.1	28.3	3830.6	324.7	900	–	–	–
Yucca whipplei	2344	156	–	–	1875	156	1562	469	937	–	1719	156
	1828.9	50	–	–	4682.4	48	7735	226.2	4548.3	–	6295	100

— = not present

Table 3. Probability that the differences in distribution of the variables occurred by chance in 2-way ANOVA

	Cover	Density	Size
Reproductive mode	0.0000	0.6918	0.0000
Fire intensity[a]	0.6458	0.4673	0.1974
Reproductive mode	0.0000	0.4200	0.0000
Abundant species (1–9)	0.0020	0.0000	0.0182
Reproductive mode	0.0691	0.9186	0.2552
Rarer species (10–17)	0.6140	0.5834	0.9810

[a] Reaction intensity 12,000 vs. 9,800 kcal/min/m^2

viduals) (Table 1). The plant density of sprouters and seeders is not markedly different but resprouts are individually larger (Table 2).

Resprouts cover a significantly greater area and are significantly larger than seedlings on all sites, regardless of fire intensity (Table 3). Resprouts of the nine most frequent species were significantly larger and had greater cover than seedlings, and there were significant differences in cover, density, and size between species. With the eight less frequent species neither differences between resprouts and seedlings nor between species were significant. Clearly, the post-fire recovery of these sites is primarily due to the resprouting of individual shrubs which are faster growing and thus larger than seedlings. Average foliar cover of resprouts exceeded that of seedlings by factors ranging from 9 to 63 on the six sites. A secondary contribution to recovery was made by seedlings. The small size of the seedlings suggests that they may have arisen from seeds produced by resprouting individuals in the first post-fire year, as observed by Westman et al. (1981).

Discussion

On these sites the main regeneration strategy for coastal sage shrubs is by resprouting. Westman (1981b) reported that of the 25 most widespread and dominant shrubs or small trees found in coastal sage scrub, all demonstrated crown sprouting abilities. All 17 shrub species encountered on our sites also resprouted following fire. This contrasts with Hanes' (1971) finding that only 50% of the 59 shrubs in coastal chaparral can resprout.

The potential vigor of resprouting appears to be a characteristic which varies widely within genera and even among sub-species or ecotypes. On sites where *Salvia leucophylla* occurred, foliar cover of its resprouts exceeded that of seedlings by an average factor of 268, in contrast to *S. mellifera* whose cover ratio for resprouts/seedlings was 6. Similarly the cover ratio for *Eriogonum cinereum* was 156 vs. 1 for *E. fasciculatum*. *Encelia californica* resprout cover surpassed that of seedlings by nearly nine-fold; in contrast, a single individual of the congener *E. farinosa* resprouted at an inland site which it had dominated prior to a fire of similar intensity. No individuals of *Eriogonum fasciculatum* or *Artemisia californica* resprouted at another inland site, despite experiencing a cooler burn (Westman et al. 1981). Intraspecific differences in fire mortality are probably ascribable to a host of physiological, morphological, and environmental variables such as rooting depth, carbohydrate storage, location of adventitious buds, moisture status of soil and plant at time of fire, fire intensity, plant size, and ecotypic differences.

Keeley and Zedler (1978) characterize sprouting and nonsprouting as two ends of a regeneration strategy continuum for chaparral shrubs, many of which reproduce almost exclusively by one means or the other. Coastal sage shrubs, like several chaparral shrubs (e.g. *Adenostema fasciculatum*), occur at an intermediate location on this continuum although biased toward the resprout end. Westman et al. (1981) found that following fire shrub seedling reproduction does not become common until the second year and suggested that the seedlings arose from resprouting shrubs fruiting in the first year. Keeley (unpublished data) also reports an increase in seedling density from 2,000/ha in the first year to 1,150,000/ha in the second. This could be due to suppression of shrub seedlings by post-fire annuals in the first year, or to high seed mortality in the soil during the fire. Thus most of the cover in a mature stand of coastal sage scrub on the studied sites will have arisen as either crown sprouted individuals or their progeny.

Keeley (1977) has speculated that the main selective pressure for the obligate seeding strategy in chaparral has been the low fire frequency in certain areas of southern California. The region of southern California of lowest natural fire frequency is the coastal ranges – the area which supports the greatest abundance and diversity of nonsprouting chaparral species. By contrast, the coastal sage shrubs on the lower elevation maritime sites appear to resprout more vigorously than at higher elevation inland sites where lightning fires are more frequent. Additionally, those sage scrub species that we found to resprout most readily (i.e. *Eriogonum cinereum, Salvia leucophylla,* and *Encelia californica*) occur most commonly in the southern coast ranges.

Resprouting in coastal sage may be favored even under this low fire frequency regime because of poor seed survival during fire. Westman (1981c) has argued that coastal sage species continually recruit seedlings between fires, in part because of their open canopy, and Keeley (personal communication) has found no inhibition of germination in coastal sage shrubs. Assuming a functional relationship in seed coat properties favoring dormancy and survival during fire, we believe that continual seedling recruitment is linked to greater fire mortality in the seed bank.

Regeneration by resprouting is a strategy well suited to the structure and function of coastal sage communities. In a community in which evapotranspirative stress reduces the growth of plants, maintains an open canopy, and may indirectly cause shrub mortality, the fittest individuals will reproduce continually and in the post-fire condition. These circumstances should lead to the strategy of producing non-dormant/non-fire resistant seeds, assuming a structural trade-off, and resprouting from root crowns.

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