Iowa Research Online
The University of Iowa's Institutional Repository

Department of Geography Publications

1-1-1985

Post-Fire Succession in Californian Coastal Sage Scrub: the Role of Continual Basal Sprouting.

George P. Malanson

W. E. Westman

Author Posting. Copyright © American Midland Naturalist, 1985. This article is posted here by permission of the publisher for personal use, not for redistribution.

The definitive version was published in *American Midland Naturlist*, 113 (1985), pp. 309-318. doi:10.2307/2425576

Hosted by Iowa Research Online. For more information please contact: lib-ir@uiowa.edu.

The University of Notre Dame

Postfire Succession in Californian Coastal Sage Scrub: The Role of Continual Basal Sprouting
Author(s): George P. Malanson and Walter E. Westman
Source: *American Midland Naturalist*, Vol. 113, No. 2 (Apr., 1985), pp. 309-318
Published by: The University of Notre Dame
Stable URL: http://www.jstor.org/stable/2425576
Accessed: 16/09/2010 15:49

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=notredame.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The University of Notre Dame is collaborating with JSTOR to digitize, preserve and extend access to *American Midland Naturalist.*

http://www.jstor.org

Postfire Succession in Californian Coastal Sage Scrub: The Role of Continual Basal Sprouting

GEORGE P. MALANSON[1] and WALTER E. WESTMAN[2]
Department of Geography, University of California, Los Angeles 90024

ABSTRACT: Dominant shrub species of coastal sage scrub in coastal southern California are able to produce shoots from their base on a continual basis in the absence of fire or other major defoliation. As a result, each shrub becomes a population of mixed-aged branches (ramets) and extends its duration in the canopy beyond the age of any of its above-ground phytomass, reduces the incidence of senescence, and permits an individual (genet) to survive during long fire-free intervals. A computer simulation of succession in coastal sage scrub under differing fire intervals shows that continual basal sprouting may be significant in influencing the long-term composition of the vegetation.

INTRODUCTION

Studies of postfire regeneration in California coastal sage scrub have emphasized the importance of both postfire resprouting and between-fire seedling establishment in maintaining populations of the shrubs that dominate this Mediterranean-climate community (Westman *et al.,* 1981; Malanson and O'Leary, 1982; Westman, 1982). Here we examine a third phenomenon: the continual production of new basal branches from epicormic buds at shrub bases during fire-free intervals. We document the extent of such sprouting and its effect on population structure and succession in coastal sage scrub.

Californian coastal sage scrub is dominated by low (0.5-2.0 m), shallow-rooted, facultatively drought-deciduous malacophyllous shrubs. Kirkpatrick and Hutchinson (1977), Axelrod (1978) and Westman (1983a) described the major associations, dominated by *Artemisia californica, Eriogonum fasciculatum, Salvia mellifera* and *S. leucophylla.* Each shrub produces many basal branches from a root crown. This growth form is predominant in the community and is similar to that of many chaparral shrub species, although the development of a burl is never as great.

All shrub species so far observed in Californian coastal sage scrub are able to resprout from root crowns or stem bases within the first growing season following fire (Westman, 1981a; Westman *et al.,* 1981; Malanson and O'Leary, 1982). Sage scrub dominants have an uneven age structure in mature stands (*e.g.,* 25-year-old) based on xylem ring counts of the largest basal branch (Westman, 1982). Such data could be interpreted as evidence for continual seedling reproduction, continual production of basal sprouts, or both (Westman, 1982; *cf.*, Gray, 1982). Although seedlings of coastal sage shrubs are observable in mature stands and are capable of germinating in the absence of fire, the relative importance of seedling reproduction vs. continual basal sprouting to the maintenance of the mixed-aged structure has not been previously assessed.

While basal sprouting in the first growing season after a fire is a phenomenon reported for both chaparral and coastal sage scrub analogues in all Mediterranean-climate regions (*see, e.g.,* Kruger, 1983; Westman, 1983b), such sprouting was previously reported to occur only following stress-induced defoliation by fire or frost (Mooney, 1977). We present evidence for the continual production of basal sprouts in the absence of acute stress, and explore the implications of this finding for long-term community structure by means of a simulation model of postfire succession in coastal sage scrub (Malanson, 1984a).

The occurrence of continual basal sprouting in dominant shrub species of coastal

[1] Present address: Department of Geography, Oklahoma State University, Stillwater 74078.
[2] Present address: NASA Ames Research Center M/S 242-4, Moffett Field, California 94035.

sage scrub was examined using field observations and experimental manipulations in the field and laboratory. All field observations were made in the coastal Santa Monica Mountains near Los Angeles (Deer, Little Sycamore, Puerco and Tuna canyons, and Arroyo Sequit). The species examined are the dominant shrub species of the coastal sage scrub in that area. They are usually found in two distinct subassociations (Westman, 1983a; Malanson, 1984b) but can be found together. The date of last fire on each site was obtained from records of the Los Angeles and Ventura County fire departments.

FIELD AND LABORATORY OBSERVATIONS AND EXPERIMENTAL MANIPULATIONS

(1) *Age of all stems per shrub.*—Every basal branch of two *Artemisia californica,* one *Salvia leucophylla* and three *S. mellifera* shrubs on sites of 12, 27 and 25 years age, respectively, and on which they were dominant, were cut and xylem rings counted to determine whether basal shoots were of equal age. This sample resulted in similar numbers of branches per species. Xylem rings should accurately represent annual growth because of the distinct seasonality of the Mediterranean climate. The dimorphic leaf structure of coastal sage shrubs (Westman, 1981b) results in a gradual reduction in foliar cover during the summer and makes double ring production unlikely. The rapid growth response of these shrubs to rainfall also makes the lack of a ring in any year unlikely. Nevertheless, the possibility of double or missing rings cannot be ruled out. At least two counts per stem along an axis of maximum growth were made under magnification. On some older sites *A. californica* cannot be dated because of stem decay and parasitism, but the four largest *A. californica* individuals on a 25-year-old site were successfully dated. The correspondence of number of rings with site age was also examined for *S. mellifera* on an 8-year-old site. The small samples of *A. californica* and *S. mellifera* indicate that the number of xylem rings is usually less than the age of the site, even when sampling for the oldest possible individual (Fig. 1).

(2) *Population age structure; seedling reproduction in mature stands; resprouting from cut stems of mature shrubs in field.*—On the same sites the structure of the populations of *Artemisia californica, Salvia leucophylla* and *S. mellifera* were established by cutting the single largest basal branch of every individual on the site. These samples totaled 79, 88 and 186 individuals on the sites at ages of 11, 25 and 23 years for these three species, respectively. On each of these sites we also sampled seedlings in 4 2 x 2 m quadrats, placed randomly. Two years later we re-examined 50, 50 and 100 individuals of the three respective species for the incidence of resprouting in the area of the cut.

(3) *Resprouting from undisturbed mature shrubs.*—Shrubs of *Artemisia californica, Encelia californica, Eriogonum cinereum, Salvia leucophylla* and *S. mellifera* were examined in mature sites (ca. 25 years since fire) for the presence of developing epicormic buds at shrub bases and for the existence of shoots of different sizes and ages arising from these buds.

(4) *Resprouting from young clipped shrubs in field.*—Resprouts and seedlings of the above species on a 2-year-old site were clipped to the ground in the autumn and the presence of resprouts observed the following spring.

(5) *Resprouting from young clipped shrubs in pots.*—Two-year-old seedlings raised in pots under nursery and greenhouse conditions (fertilized, watered) were clipped to the base and the presence of resprouts observed 1 month later, in spring. The five species listed above plus *Eriogonum fasciculatum, Lotus scoparius, Rhus laurina* and *Quercus agrifolia* were observed.

SIMULATION MODELING

In addition to the above observations and experiments, we ran computer simulations of postfire reproduction under different fire frequency regimes using a model of postfire succession developed for coastal sage scrub species in the Santa Monica Mountains (Malanson, 1984a). The model uses Leslie matrices to simulate scramble competition (*cf.*, Whittaker, 1975) for a fixed resource base for the five species listed in (3)

above (Fig. 2). Observed resprouting rates (proportion of adults) following fire were entered in the model. For seedling reproduction, fertility functions in the Leslie matrices were based on observations of postfire seedling establishment (Malanson and O'Leary, 1982). As individuals aged, their seedling production was modeled to increase as a function of plant size. Canopy size of individual shrubs increased with age. In the simulation, growth continued with age until foliar cover for all species reached 100%, at which point further growth occurred only as deaths reduced canopy cover. Scramble competition for canopy openings occurred, with extensions of foliar cover depending upon species' existing relative cover values and growth rates.

Survivorship rates were calculated using a Weibull function to approximate Deevey (1947) Type I survivorship for resprouts and Type III survivorship for seedlings (*cf.*, Pinder *et al.*, 1978). The Weibull function is controlled by two coefficients. The b coefficient controls the end-point of the distribution and the c coefficient controls curve shape. The Type I curves were calculated with a c coefficient of 5, and the Type III

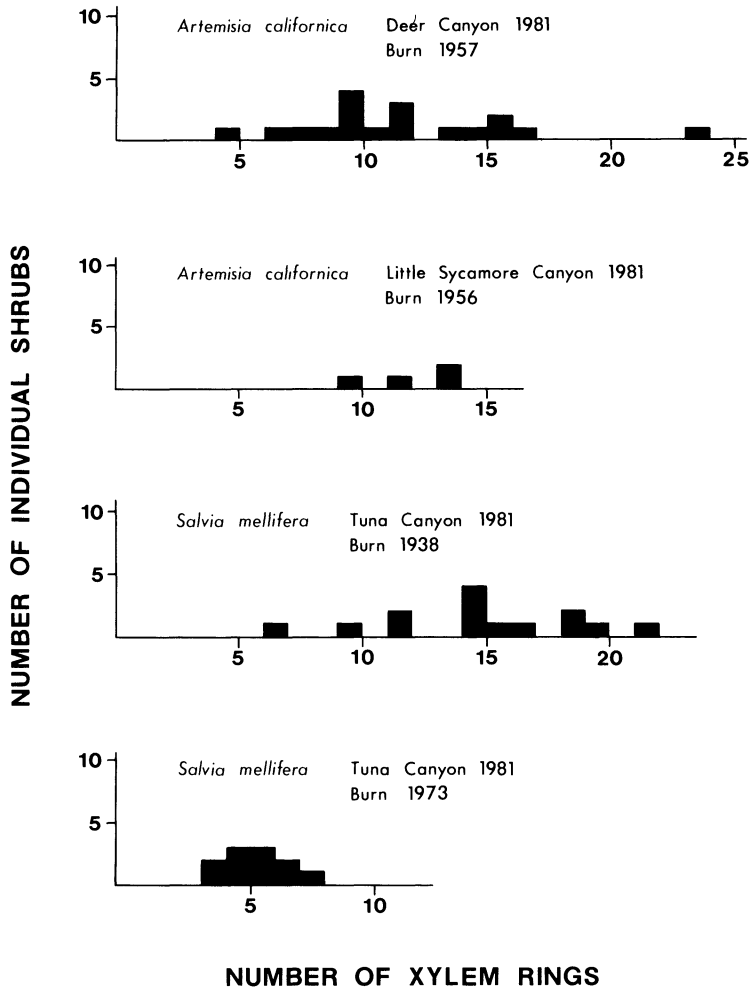

Fig. 1.—Age pf selected large shrubs by xylem rings of single largest basal branch. Years since last fire shown. Sampled in 1981. Site ages from top to bottom: 24, 25, 43, 8 years

curves with a c coefficient of 0.3 for all species in this test. We calculated the b coefficient for cases where (1) individual shrub survivorship was limited to the age indicated by the oldest cut stem of the species (*Artemisia californica* 20 years; *Encelia californica* 20 years; *Eriogonum cinereum* 20 years; *Salvia leucophylla* 30 years; *S. mellifera* 30 years); and (2) survivorship was extended to 60 years for all species. For *Encelia californica* and *Eriogonum cinereum* even 20 years' longevity is beyond the ages of individual branches. These two conditions of survivorship represent cases where (1) individual shrubs are short-lived (20-30 years), or (2) individuals persist beyond the longest fire-free periods observed in the Santa Monica Mountains in this century (ca. 40 years; Radtke *et al.*, 1982). We examined the differences in community composition for these species modeled under the two conditions of longevity

The model calculates the foliar cover of the five species at 5-year intervals. Sequences of fixed 10-, 20- and 40-year fire intervals for 200-year periods and 30-year intervals for 210-year periods were simulated.

RESULTS

The results indicate that even-aged stands of shrubs comprised of branches of mixed ages arise largely due to continual basal sprouting in the absence of fire. Results of the five observations and the simulation are listed below.

FIELD, LABORATORY AND EXPERIMENTAL OBSERVATIONS

(1) *Age of all stems per shrub.*—The six individuals shown in Figure 3 exhibit mixed ages of basal branches per individual. Each shrub produces new basal branches almost every year.

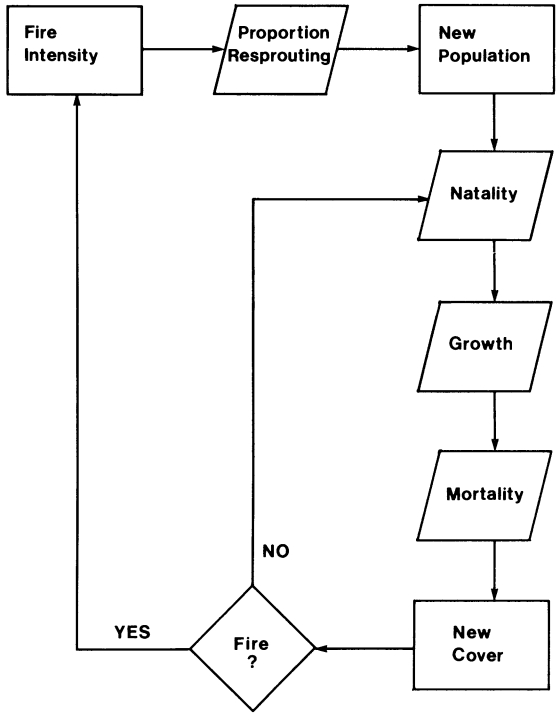

Fig. 2.—Outline of the simulation procedure incorporating Leslie matrices in the interior loop and fire intensity in the exterior loop

(2) *Population age structure; seedling reproduction in mature stands; resprouting from cut stems of mature shrubs in field.*—The population structures of *Artemisia californica, Salvia leucophylla* and *S. mellifera* based on the largest basal branch are not even-aged (Fig. 4). These structures could indicate either that the populations are made up mostly of seedlings which arose during the various years since the last fire, or that the largest basal branch, assumed to be the oldest, does not represent the age of the shrub root crown. Given the high proportion of resprout to seedling cover in early postfire years, approximately 19:1, reported by Malanson and O'Leary (1982), the lack of dead shrubs on coastal sage sites in general (*cf.*, Gray, 1983), and the relatively small number or absence of seedlings of at least some dominants (*e.g., S. leucophylla*) on mature sites (Table 1), continual seedling reproduction as the sole cause of the uneven age distribution appears unlikely. The clipped shrubs resprouted vigorously 1 year later (Table 2).

(3) *Resprouting from undisturbed mature shrubs.*—Sprouts can be observed to arise from basal buds on most mature shrubs of the species examined (Fig. 5). These sprouts clearly contribute to the variable sizes of the basal stems.

(4) *Resprouting from young clipped shrubs in field.*—All 2-year-old resprouts clipped in the field resprouted; no seedlings resprouted. Zedler *et al.* (1983) found that burned 1-year-old seedlings of *Artemisia californica* did resprout.

(5) *Resprouting from young clipped shrubs in pots.*—All clipped seedlings from the experiment, except those of *Eriogonum cinereum,* produced new basal sprouts within 1 month.

SIMULATION MODELING

The computer simulations project varying levels of importance for the five competing species (Fig. 6). Some species are more successful at shorter fire intervals; these spe-

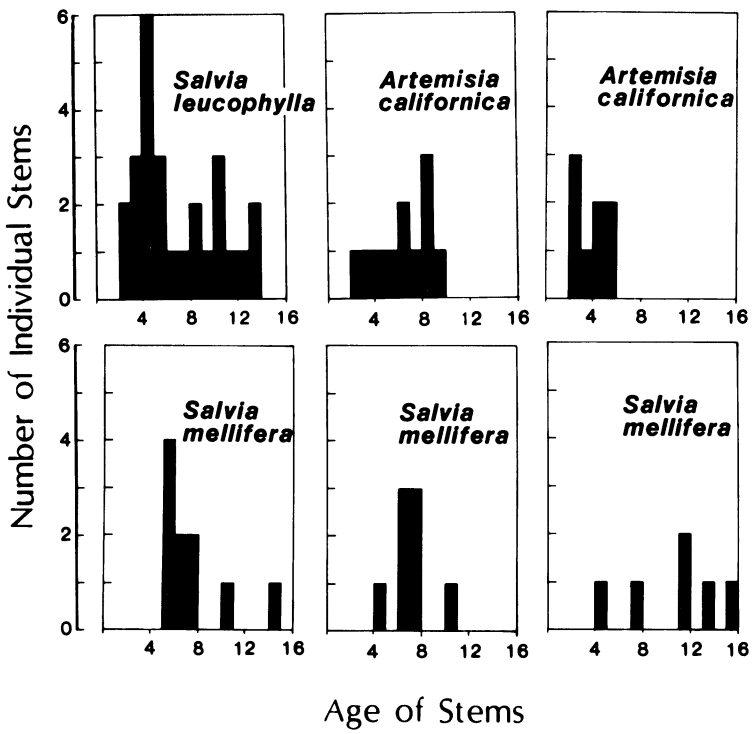

Fig. 3.—The age distribution of all basal branches of six individual shrubs

cies are generally more vigorous resprouters. Other species, resprouting less abundantly, are more successful at longer fire intervals.

Without the assumption of continual basal sprouting, the projected community is not realistic (Fig. 6a). *Eriogonum cinereum* and *Salvia leucophylla* are extant in small numbers after the 200-year sequence of fires only at 10-year fire intervals. *Encelia californica* remains extant at 10- and 20-year fire intervals. No species survive the sequences of 30- and 40-year intervals and *Artemisia californica* and *S. mellifera* are never extant after any series of fires. Most of the population decline occurs in the first few intervals. When longevity is extended to a possible 60 years due to continual basal sprouting, all species are much more abundant (Fig. 6b) except *S. mellifera*. Since *S. mellifera* is abundant on older sites in the field, it is likely that seedling survivorship postulated in the model ($c = 0.3$) underestimates true survivorship rates in this species. Given the modeling results and seedling data of Table 1, it would appear that dependence on seedling reproduction decreases in the order *A. californica* > *S. mellifera* > *S. leucophylla*.

Field observations indicate that sites ca. 25 years old in the Santa Monica Mountains contain a mixture of the above shrub species without signs of population decline

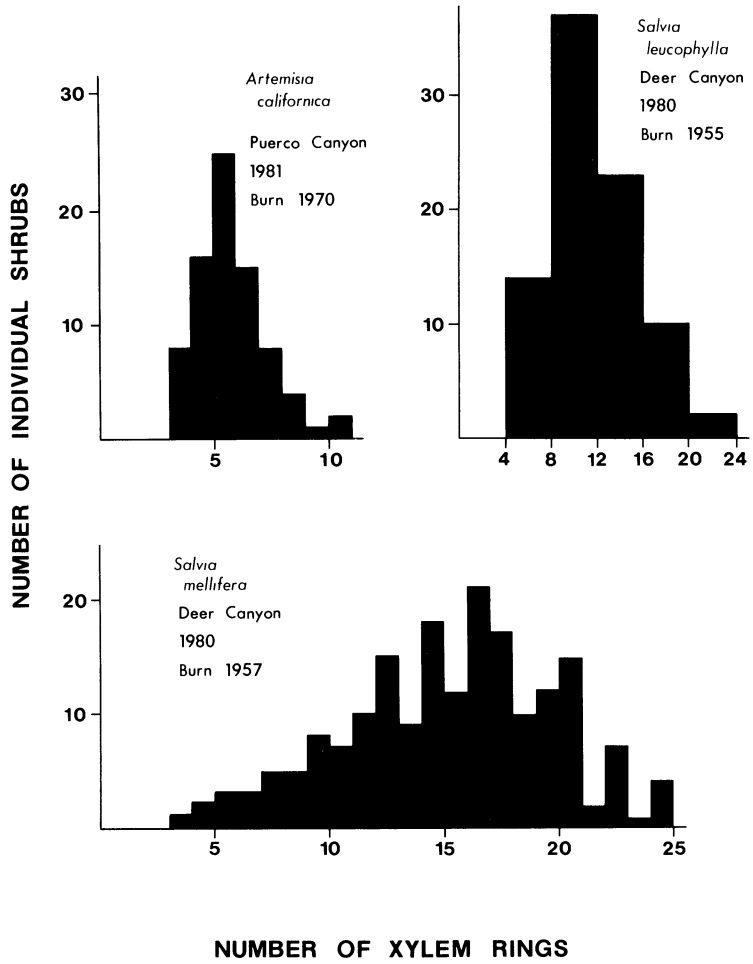

Fig. 4.—Population structures by xylem rings of single largest basal branch

(Westman, 1981a, Westman *et al.*, 1981, Gray 1983). The simulation reflects these observations only when it incorporates the assumption of extended longevity derived from the process of continual basal sprouting. These projections thus indicate that, within the limits of the model, the extended longevity attributable to continual basal sprouting is essential to the maintenance of a particular species composition in successional sequences. The recruitment of seedlings is not sufficient to maintain species populations if individual genets are as short-lived as their oldest branches. The simulation cannot be said to quantify the importance of basal sprouting, but it does show that this mechanism can be crucial to the stability of the community during long fire-free intervals.

DISCUSSION

It is now clear that, as with perennial grassland (*cf.*, Harper, 1977), one must speak of the "age" of coastal sage scrub vegetation in terms of the distinct ages of plant parts. Belowground parts may vary in age from many years older (resprouted plants) to many years younger (seedlings or adventitious stock) than the age of the site since last fire. Aboveground ramets on species such as *Artemisia* and *Salvia* will typically last only 20 or 30 years, respectively, in the absence of fire. Basal crown sprouting will continue to replenish aboveground parts so that basal stems in a stand can be a variety of ages. In other species, such as *Encelia californica* and *Eriogonum cinereum,* it is common for many of the aboveground stems to die and arise anew on a much shorter cycle. The mixed-age structure of basal stems earlier reported for *S. mellifera* (Westman, 1982) may have arisen from a combination of continual seedling reproduction and continual basal sprouting. The low number of *Salvia* seedlings observed in mature stands and the frequent occurrence of continual basal sprouting together suggest that basal sprouting may be the predominant mechanism of rejuvenation of shrub parts in coastal sage scrub between fires.

Indeed, the observation of resprouting from clipped sclerophyllous chaparral species such as *Quercus agrifolia* and *Rhus laurina* suggests that continual basal sprouting may occur in many species capable of basal sprouting immediately after fire. If this is the case, the increased senescence (abundance of dead plants) observed in older chaparral relative to coastal sage may be due in part to the lower frequency of resprouting in coastal chaparral (ca. 50%, the others being obligate seeders; Hanes, 1971) than coastal sage scrub (c. 100%; Westman, 1982). Schlesinger and Gill (1978) reported 50% mortality of *Ceanothus megacorpus* on a 21-year-old site of chaparral dominated by even-aged individuals of this obligate seeder. The obligate seeders regenerate like forest (nonsprouting) trees, the sprouters like perennial grasses, so that in terms of generation strategies much

TABLE 1.—Number of seedlings and adults observed on relatively mature sites of coastal sage scrub. Adults were counted within 625m² plots, seedlings were observed in four 4 m² plots and results extrapolated to 625 m²

Species	Number per 625m² Seedlings	Adults	Years since last fire on site
Artemisia californica	547	79	11
Salvia leucophylla	0	88	25
S. mellifera	39	186	23

TABLE 2.—Number of mature shrubs clipped at ground level and number of these which resprouted 2 years later

Species	Years since last fire at site	Number of shrubs clipped	Number of shrubs which resprouted 2 years later
Artemisia californica	11	50	40
Salvia leucophylla	25	50	45
S. mellifera	23	100	91

chaparral may be analogous to a forest savanna of mixed sprouters and obligate seeders, the coastal sage scrub to a perennial grassland of continual basal sprouters.

The greater abundance of continually sprouting species in coastal sage communities compared to chaparral may be explained on the basis of the differences in the habitats they occupy. Because of the lower precipitation and/or greater evapotranspirative stress in coastal sage habitats, these sites dry out earlier in the season. Shallow roots, thin leaves and rapid growth of shoots of low-density wood allow coastal sage species to respond quickly to the onset of rains. These subligneous shoots do not last as long as those of evergreen chaparral (*cf.*, Keeley, 1975). Furthermore, the shorter growing season results in lower fuel loads (Kessell and Cattelino, 1978) and potentially longer fire-free intervals. An individual which cannot rejuvenate its aboveground structure through continual resprouting is vulnerable to overtopping and replacement by another individual, possibly of a different species (*cf.*, Gray, 1983). Continual resprouting is thus advantageous to rapidly growing species with short-lived aboveground parts, as is demonstrated in the life histories of perennial grasses and herbs. Continual basal sprouting helps to maintain existing community composition between fires, enhancing "ecosystem inertia" (resistance to change; Westman, 1978).

It seems likely that similar contrasts will be found in other evergreen vs. malacophyllous Mediterranean-climate shrublands. If so, the implications for vegeta-

Fig. 5.—Shoots of different sizes arising from the base of a mature individual of *Salvia mellifera*

tion dynamics and fire management are widespread. The fire interval that will maintain malacophyllous Mediterranean-climate shrublands quite likely will differ from the optimum interval for evergreen shrublands, and may be longer than previously assumed.

Acknowledgments.—The clipped 2-year-old seedlings in pots which were observed are part of an ongoing experiment by K. Preston, L. Weeks and W. E. Westman. S. C. Coon assisted in field work. J. E. Keeley and S. C. Keeley commented on an earlier draft of the manuscript. This research was partially supported by a grant from the Division of Environmental Biology, National Science Foundation.

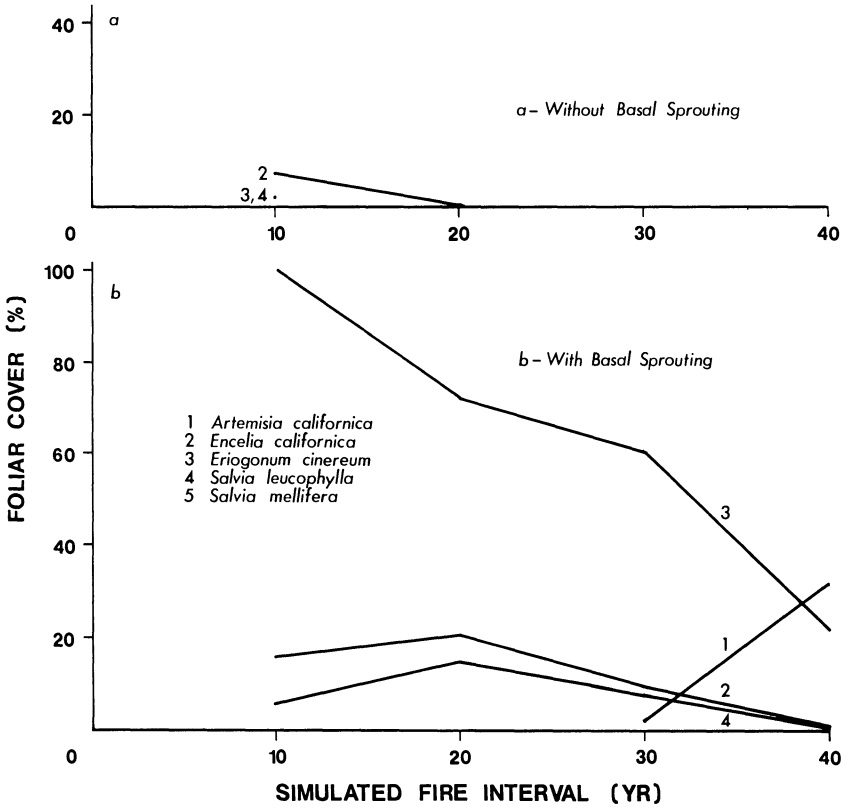

Fig. 6.—Percent foliar cover of five shrub species of coastal sage scrub after 200-210 years of periodic burning at one of four fire intervals as projected by simulation: a. model projections not assuming continual basal sprouting; b. model projections assuming continual basal sprouting

LITERATURE CITED

AXELROD, D. 1978. The origin of coastal sage vegetation, Alta and Baja California. *Am. J. Bot.*, **66**:1117-1131.

DEEVEY, E. S. 1947. Life tables for natural populations of animals. *Q. Rev. Biol.*, **22**:283-314.

GRAY, J. T. 1982. Community structure and productivity in *Ceanothus* chaparral and coastal sage scrub of southern California. *Ecol. Monogr.*, **52**:415-435.

_____. 1983. Competition for light and a dynamic boundary between chaparral and coastal sage scrub. *Madroño*, **30**:43-49.

HANES, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.,* **41**:27-52.

HARPER, J. L. 1977. Population biology of plants. Academic Press, New York. 892 p.

KEELEY, J. E. 1975. Longevity of nonsprouting *Ceanothus. Am. Midl. Nat.,* **93**:504-507.

KESSELL, S. L. AND P. J. CATTELINO. 1978. Evaluation of a fire behavior information integration system for southern California chaparral wildlands. *Environ. Manage.,* **2**:135-157.

KIRKPATRICK, J. B. AND C. F. HUTCHINSON. 1977. The community composition of Californian coastal sage scrub. *Vegetatio,* **35**:21-33

KRUGER, F. J. 1983. Plant community diversity and dynamics in relation to fire, p. 446-472. *In*: F. J. Kruger, D. T. Mitchell, J. U. M. Jarvis (eds.). Mediterranean-type ecosystems. The role of nutrients. Springer-Verlag, Berlin.

MALANSON, G. P. 1984a. Linked Leslie matrices for the simulation of succession. *Ecol. Modeling,* **21**:13-20.

_____. 1984b. Fire history and patterns of Venturan subassociations of Californian coastal sage scrub. *Vegetatio:* **57**:121-128.

_____ AND J. F. O'LEARY. 1982. Post-fire regeneration strategies of Californian coastal sage shrubs. *Oecologia,* **53**:355-358.

MOONEY, H. A. 1977. Frost sensitivity and resprouting behavior of analogous shrubs of California and Chile. *Madroño,* **24**:74-78.

PINDER, J. E., J. G. WEINER AND M. H. SMITH. 1978. The Weibull distribution; a new method of summarizing survivorship data. *Ecology,* **59**:175-179.

RADTKE, K. W. H., A. M. ARNDT AND R. H. WAKIMOTO. 1982. Fire history of the Santa Monica Mountains, p. 438-443. *In:* C. E. Conrad and W. C. Oechel (eds.). Dynamics and management of Mediterranean-type ecosystems. *U.S. For. Serv. Gen. Tech. Rep. PSW-58.*

SCHLESINGER, W. H. AND D. S. GILL. 1978. Demographic studies of the chaparral shrub, *Ceanothus megacarpus,* in the Santa Ynez Mountains, California. *Ecology,* **58**:1256-1263.

WESTMAN, W. E. 1978. Measuring the inertia and resilience of ecosystems. *BioScience,* **28**:705-710.

_____. 1981a. Diversity relations and succession in Californian coastal sage scrub. *Ecology,* **62**:170-184.

_____. 1981b. Seasonal dimorphism of foliage in Californian coastal sage scrub. *Oecologia,* **51**:385-388.

_____. 1982. Coastal sage scrub succession, p. 91-99. *In*: C. E. Conrad and W. C. Oechel (eds.). Dynamics and management of Mediterranean-type ecosystems. *U.S. For. Serv. Gen. Tech. Rep. PSW-58.*

_____. 1983a. Xeric Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. *Vegetatio,* **52**:3-19.

_____. 1983b. Plant community structure—Spatial partitioning of resources, p. 417-445. F. J. Kruger, D. T. Mitchell, J. U. M. Jarvis (eds.). *In*: Mediterranean-type ecosystems. The role of nutrients. Springer-Verlag, Berlin.

_____, J. F. O'LEARY AND G. P. MALANSON. 1981. The effects of fire intensity, aspect, and substrate on post-fire growth of Californian coastal sage scrub, p. 151-179. *In*: N. S. Margaris and H. A. Mooney (eds.). Components of productivity of Mediterranean regions. W. Junk, The Hague.

WHITTAKER, R. H. 1975. Communities and ecosystems, 2nd ed. Macmillan, New York. 359 p.

ZEDLER, P. H ., C. R. GAUTIER AND G. S. MCMASTER. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology,* **64**:809-818.

SUBMITTED 23 JANUARY 1984 ACCEPTED 2 JULY 1984