

Coastal Sage Scrub Succession¹

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Coastal sage scrub is a soft-leaved (mesophyllous) shrubland community which occurs on sites drier than those of chaparral in the Mediterranean-climate portions of California. While basic patterns of succession in Californian chaparral have been known for some time (Sampson 1944; Horton & Kraebel 1956; Hanes 1971, 1977; Schlesinger & Gill 1978, 1980), those of coastal sage scrub have only recently begun to be examined (Westman 1980a, Westman et al. 1981). In the absence of more information, managers of southern California shrublands have had little alternative but to assume that processes of succession in coastal sage scrub were analogous to those in chaparral and that the two community types could be treated identically for management purposes. Recent information on ecosystem structure and dynamics in coastal sage scrub (Mooney et al. 1977b; Westman 1979a, 1981 a, b, c, d) leads to the conclusion that coastal sage scrub exhibits patterns of succession quite distinct from those of chaparral in virtue of differences in its structure, physiognomy and habitat. These differences suggest the need for distinctive management practices for the type. This paper contrasts structural and dynamic features of coastal sage scrub with those of chaparral in order to highlight how these differences lead to distinctive successional patterns.

DISTRIBUTION OF THE COMMUNITY TYPES

Coastal sage scrub occurs discontinuously from the latitude of San Francisco south to El Rosario in Baja California (Fig. 1). It is found most extensively in the lower elevations of coastal southern California, but occurs up to 1300m in elevation in the Coast Ranges (e.g. Cuyamaca Mountains, San Diego County), and intergrades to Mojave desert vegetation to the east and to Sonoran vegetation in Baja California. Kirkpatrick and Hutchinson (1977) and later Axelrod (1978) and

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Abstract: Unlike chaparral, shrubs of coastal sage are capable of continual seedling reproduction. As a result, mixed-aged stands form which show little senescence. Litter turnover is twice as rapid. The more open sage scrub canopy permits persistence of a diverse herb layer into mature communities. Crown sprouting potential is greater, but heat tolerance of root crowns may be more variable. Higher volatile oil contents compensate for lower fuel loads so that fire frequencies in sage scrub and coastal chaparral are comparable (once per 20 y). Seasonal dimorphism, poikilohydric behavior and leaf deciduousness permit sage species to survive in drier habitats and occupy dry chaparral sites in the early years following fire.

Westman (1981b) recognized three major floristic associations in southern coastal sage scrub: a coastal group (Venturan), a cismontane inland group (Riversidian), and a Baja-influenced group (Diegan). The Diegan association shows the increased influence of succulents, and is probably best treated as a distinct community type (coastal succulent scrub: Mooney & Harrison 1972, Mooney 1977; Mooney et al. 1977b; maritime cactus scrub: Philbrick & Haller 1977). North of Point Conception, the coastal shrubland shows an increased abundance of evergreen shrubs (*Baccaris pilularis*, *Arctostaphylos* spp.), and is termed northern coastal scrub (Heady et al. 1977). The southern

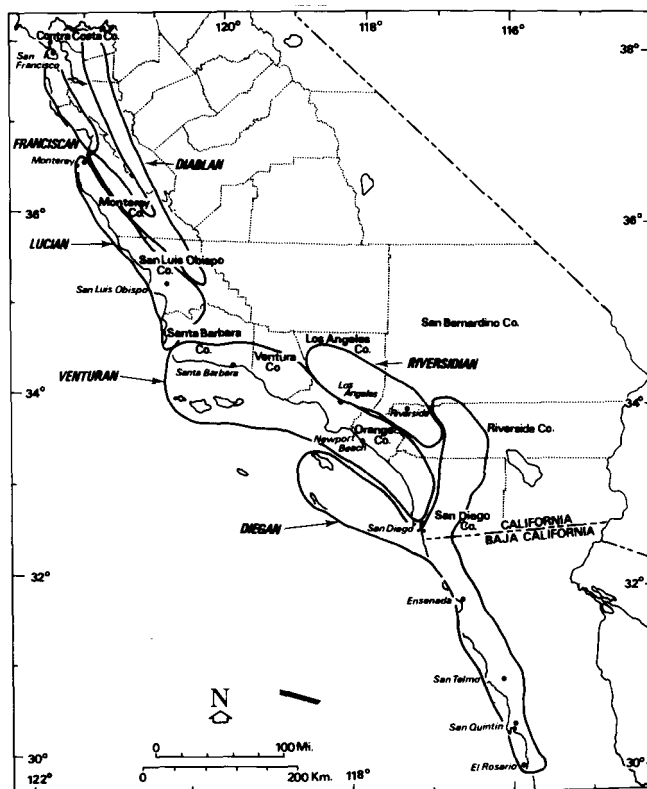


Figure 1. Approximate distributions of the major floristic associations within southern coastal sage scrub, after Axelrod (1978), Westman (1981b) and Westman, field observations.

coastal sage scrub, dominated by species of Salvia, Encelia, Eriogonum and Artemisia, occurs in discontinuous patches on drier slopes to its northernmost occurrence in the Mt. Diablo area. In the present paper, the term "coastal sage scrub" refers primarily to the Venturan and Riversidian floristic associations. Where evergreen chaparral is adjacent to coastal sage scrub, it is found on more mesic sites, generally at higher elevations in the Coast Ranges. It also extends to the slopes of the Sierra Nevada, and to areas north of San Francisco (Hanes 1977).

PHYSIOGNOMIC ATTRIBUTES AND THEIR CONSEQUENCES FOR SUCCESSION

Leaf Structure

Chaparral shrubs have sclerophyllous leaves, typically thickly cuticularized and more resistant to water loss than the thin, mesophyllous leaves of coastal sage scrub. A few important chaparral dominants (e.g. Adenostoma fasciculatum) have narrow leaves, whereas virtually all mesophyllous sage dominants have broader leaves. The lower transpiration rates of chaparral leaves generally result in lower photosynthetic rates per unit leaf mass (Harrison et al. 1971). While net primary productivity on an areal basis is 1.4 - 3.3-fold greater for chaparral than sage scrub (chamise chaparral: Mooney & Rundel 1979; Ceanothus chaparral: Schlesinger & Gill 1980; Venturan sage: Gray & Schlesinger. 1981), the growth is spread more evenly over the year, whereas it is limited to the 5 - 6 months following onset of rains in sage scrub (Gray & Schlesinger 1981). While the latter is due in part to the drought-intolerant mesophyllous leaf structure, shallower roots and lower surface soil moisture stores also contribute to the shorter growing season of sage scrub. An implication of the mesophyllous leaf structure for succession is that sage scrub recovery is more likely to be sensitive to the time of year of applied stress than is chaparral. Thus sage scrub would probably suffer less damage to energy stores and recovery potential from defoliation stresses (grazing, fire, air pollution) occurring from June to November, and more from December to May, than chaparral.

Winner and Mooney (1980) have documented the increased susceptibility of the mesophyllous leaves of sage to SO₂ damage relative to sclerophyllous chaparral leaves. Suggestive evidence for damage to sage scrub in the field has been reported for SO₂ by Westman & Preston (1980) and for ozone by Westman (1979b). Preston and Westman are currently undertaking controlled fumigation experiments on sage species with SO₂ and ozone. A management implication is that sites of coastal sage make less desirable locations for siting of new pollution sources of SO₂ and ozone precursors than do chaparral sites.

Leaf Duration

The average life span of a leaf on a chaparral

shrub is not precisely known. Leaf half-lives for other evergreen angiosperm species have been measured at 10 - 14 months (Eucalyptus spp.: Rogers & Westman 1981), and data of Mooney and Kummerow (Mooney et al. 1977, Fig. 5-18, 5-19) suggest similar durations for Heteromeles arbutifolia and Ceanothus leucodermis. By contrast, mesophyllous sage scrub leaves invariably have shorter leaf durations (e.g. 30-50 days for Artemisia californica: Gray & Schlesinger 1981).

Coastal sage scrub has frequently been referred to as a "drought deciduous" community type (e.g. Mooney 1977; Kirkpatrick & Hutchinson 1977; Westman 1979a). Very few shrub species in this community type, however, lose all of their leaves during the dry season. A number of small tree species in the Diegan formation (Aesculus parryi and A. californica (Mooney & Bartholomew 1974); Fraxinus trifoliata; Ptelea aptera; Prunus fremontii) do show total seasonal deciduousness. Some of these (F. trifoliata, Aesculus spp.) are of Miocene age in the region (Axelrod 1978). It is quite possible that these species retained the deciduous habit as a photoperiodically triggered one from seasonally dry tropical (Axelrod 1978) or even temperate deciduous forest ancestors. These species are absent from the Riversidian and Venturan associations, where most species were probably derived from xeric margins of live-oak woodland and dry tropic scrub in the early Quaternary (Axelrod 1978). Of the shrubs in the latter associations, one of the species showing most complete summer deciduousness is Lotus scoparius. Nilsen & Muller (1980) showed that this species, while dropping some leaves due to water stress, will drop them more completely during long days than short days, suggesting a photoperiodic component to deciduousness in this species.

The most common adaptation to summer water stress in coastal sage scrub is not total deciduousness, but the production of smaller leaves on side shoots developing from the axils of larger, main-shoot leaves. In the most common pattern, main-shoot leaves are formed in the first flush of winter growth when moisture is most abundant. Almost immediately after these leaves are formed, side shoots begin to grow. Main-shoot leaves fall off acropetally as the summer drought develops, but the smaller side shoot leaves persist, to varying extents, until the following winter rainy period, whereupon the leaves fall and the shoots may now become main stems producing larger leaves, or may die. Westman (1981c) observed this pattern in most mesophyllous coastal sage shrubs examined, and Gray & Schlesinger (1981) recently described it for Salvia leucophylla and S. mellifera. This seasonal dimorphism is best developed in analogous mesophyllous shrublands in the Mediterranean (Orshan 1963), where it has been shown to be photoperiodically triggered (Margaris 1975). The phenomenon has also been reported from Chile (Montenegro et al. 1979a) and South Africa (R.M. Cowling, pers. comm. in Westman 1981c).

A third leaf-duration strategy occasionally found in sage scrub is poikilohydric behavior: the ability of leaves to wilt for long periods, and rehydrate within hours of a rainfall. This behavior is exhibited by Artemisia californica (which is also seasonally dimorphic: Westman 1981c), a shrub with one of the widest moisture tolerances and distributional ranges of any sage scrub dominant (Westman 1981b). It has also been reported from analogous vegetation in Chile (Montenegro et al. 1979b), South Africa (Gaff 1971) and Australia (Gaff & Churchill 1976).

Much remains to be investigated regarding the small, summer leaves in sage scrub species. Are these leaves physiologically more drought-tolerant than the early growing season leaves? Cunningham & Strain (1969) and Smith & Nobel (1977) have shown this to be the case for the sage/desert-margin species, Encelia farinosa, but it is not known how widespread this phenomenon is. Is production of the smaller leaves triggered photoperiodically, as in the Mediterranean? Field observations suggest not, since the sage scrub leaves can begin growth almost at the same time as main-shoot leaves expand, and because the degree of their persistence in the dry season is so variable. Indeed, in the latter feature lies their adaptiveness, since seasonal dimorphism, combined with facultative drought-deciduousness, provides an extremely flexible strategy for fine-tuning total leaf mass to moisture availability in the highly variable precipitation regime of the Mediterranean climate, while providing individual leaves that can perhaps better withstand drier conditions.

The implications of these differences in leaf duration for succession are only beginning to be explored. Westman (1981c) reported that two years following fire, there was a two-fold increase in foliar cover of seasonally-dimorphic shrubs in a coastal Venturan-formation site, relative to a 22-year-old pre-burn condition. It is possible that seasonal dimorphism provides a more effective post-fire recovery strategy on the barren, dry burned sites. This may help explain why coastal sage species frequently occupy drier post-burn chaparral sites in early years of post-fire succession (Hanes 1977). Seasonal dimorphism is restricted to mesophyllous shrubs, and does not occur in sclerophyllous shrubs, either those of the chaparral, or those which occur as associates in coastal sage communities (e.g. Rhus laurina, R. integrifolia).

Leaf oil content

More of the dominant shrub species of coastal sage scrub are highly aromatic than those of chaparral. Unfortunately, quantitative data on the relative flammability and caloric contents of leaves in coastal sage and chaparral are lacking. Chamise (Adenostoma fasciculatum) is known to have unusually high flammability due in part to its oil content. Its leaf caloric content averages 5220 cal g⁻¹ vs. a mean of 4890 cal g⁻¹ for seven other chaparral shrubs (Mooney et al. 1977a).

There are several preliminary bases for postulating a higher flammability for sage than chaparral species, all of which need further study: the high content (Tyson et al. 1974) and more widespread occurrence of volatile oils; the less dense wood; field observations suggesting that complete consumption of aboveground fuel is more common during fires in sage scrub than chaparral.

If the higher flammability of aboveground parts of sage scrub is confirmed, the evolutionary explanation for it may be sought as a corollary to the Mutch (1970) fire-dependence hypothesis. Because of a Mediterranean-type climate with a long dry season, but sufficient precipitation to support an aboveground biomass capable of sustaining fire, fires are common in both shrublands types, and adaptations for fire-dependence have evolved in both cases. The lower fuel mass and greater spacing of shrubs in coastal sage would normally act to decrease fire frequency in coastal sage relative to chaparral. This tendency could be counteracted by the evolution of a greater abundance of volatile, flammable oils in sage scrub than chaparral.

Indirect supporting evidence for this hypothesis comes from an analysis of fire frequency during the period 1930-1978 in chamise chaparral and coastal sage scrub in the western Santa Monica Mountains. In each vegetation type, 50 random points were located, and fire frequency determined. The vegetation map used was prepared by G. Nuno (1980, unpublished) based on data of the Vegetation Type Map Survey of Wieslander. This vegetation map was overlaid upon a map of fire occurrences in the Western Santa Monica Mountains (K. Radtke, unpublished). Results indicate that fire frequencies are just as great in coastal sage as in chaparral (\bar{X} occurrences for the 48-year period \pm s.e.: 2.46 \pm 0.11 for coastal sage scrub; 2.32 \pm 0.15 for chamise-chaparral) despite lower fuel loads in the former. Mean fire interval in both types was 20 years.

Twig and Stem Structure

Biomass

Wood of coastal sage shrubs is less dense and more brittle than that of chaparral (Mooney et al. 1977b; Gray & Schlesinger 1981). A consequence of this is that large woody stems do not remain standing, either dead or alive, as long as they do in chaparral. Gray & Schlesinger (1981) report a standing dead wood component of 18 percent in Venturan sage scrub, approximately half the amount for chaparral.

This feature in turn has two important implications for succession. Firstly, the more rapid return of dead wood to the litter layer provides improved nutrient turnover, and diminishes the chance for deficiencies in available nutrient stocks to develop, leading to the growth senescence reported for chaparral (Hanes 1971). A second implication is that dry fuel will be a

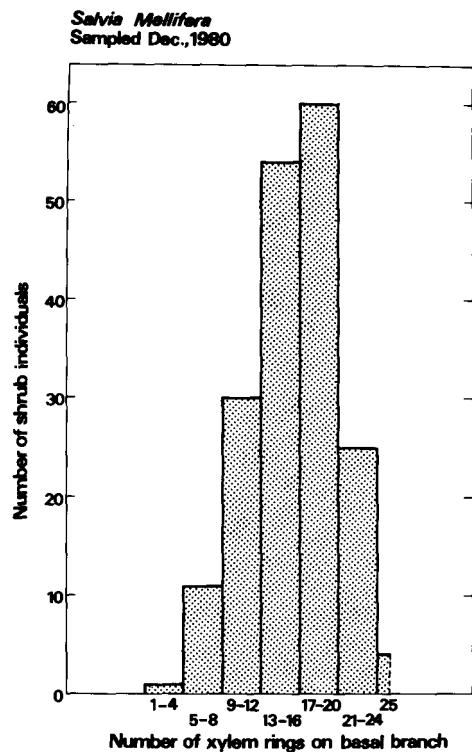


Figure 2. Numbers of individuals of *Salvia mellifera* showing a given number of xylem rings on the lowest branch, on a 23-year-old coastal Venturan site. Some individuals showed one or two extra rings as a result of the production of double rings in some years.

lower proportion of total biomass in coastal sage than chaparral, contributing to a reduction in fire intensity. This, combined with the lower living biomass per unit area, results in lower total fuel loads than chaparral. Whether these lower fuel loads result in lower fire intensities than chaparral has yet to be documented in the field and, as noted earlier, may be counteracted by higher volatile oil contents in foliage. Westman et al. (1981) calculated fire intensities on coastal sage sites, using the FIREMODS model of Albini (1976a) which is based primarily on fuel load, fuel moisture conditions and weather at the time of fire. For Venturan types reaction intensities were 170 - 200 kcal sec⁻¹m⁻²; for Riversidian types, 120 - 170 kcal sec⁻¹m⁻². These values are low for the range of values modeled in fires in older chaparral (up to 600 kcal sec⁻¹m⁻²; Albini 1976b), but the latter are not field measurements. Fire intensities clearly affect root crown survival, and subsequent patterns of successional re-growth (Westman et al. 1981).

Decomposition Rates

Whether the more rapid rate of return of wood to the litter layer in fact results in more rapid external nutrient cycling in coastal sage depends on litter decay rates. To calculate litter half-lives by the exponential decay-rate model requires assuming that the litter mass is in steady state

(Whittaker 1970). Kittredge (1955) found that litter mass in a variety of chaparral and mixed sage-chaparral types reached equilibrium in 8 - 20 years. In the 22-year-old Venturan sage site, if litter mass is assumed to be at equilibrium, litter half life is 2.2 years (data of Gray & Schlesinger 1981). The litter half-lives of two mixed sage-chaparral sites in the San Dimas Experimental Forest (Los Angeles County) were 1.8 and 3.6 years (data of Kittredge 1955), during a period when sites were 14 - 31 years old. By contrast, nine chaparral sites of the same age range exhibited a mean litter half-life of 4.4 years (range: 1.8 - 12.4 years; data of Kittredge 1955). Though site-to-site variation is great, on the average litter decay rates are twice as great in coastal sage than chaparral. The sclerophyllous nature of chaparral leaves, and their lower nutrient contents (Mooney 1977) would inhibit leaf litter decay rates relative to sage scrub, as would the higher wood density of chaparral (Gray & Schlesinger 1981).

Canopy Closure

Stems of coastal sage species rarely exceed 2 m in height, and average canopy heights more commonly range from 0.5 - 1.8 m. By contrast, chaparral canopies are commonly 2 - 3 m. The density of foliage on stems is lower in sage, resulting in lower leaf area indices per shrub (\bar{X} = 1.31 sage vs. 2.65 chaparral; Mooney et al. 1978). On drier sage sites, shrub densities fall below the point at which canopy closure is obtained. As a result of all of these factors, light penetration to ground level is greater in coastal sage than chaparral. For example, while stands of *Ceanothus* chaparral of 22 year age have irradiances immediately below the canopy of 200 - 900 microEinsteins m² sec⁻¹ (Schlesinger & Gill 1980), two stands of Venturan sage of 22 year age at Leo Carillo State Park had mean irradiances of 900 - 1000 microEinsteins m²sec⁻¹ at 10 cm above ground, and one-fifth of the 50 readings per stand were in canopy gaps (Westman, unpublished).

Understory Growth

The result of this more open canopy structure is an increased persistence of understory growth as the sage scrub matures. Thus while herbs are reduced to a very minimal occurrence in chaparral by five years after fire, they remain an important part of total cover (greater than 20 percent) for 20 years or more following fire in coastal sage (Westman 1981c).

Muller (McPherson & Muller 1969 et subseq.) has argued that shading is not a factor in herb suppression in chaparral, since herbs are absent from bare areas under canopy openings in mature chaparral. He argues instead for the role of allelopathic substances in herb suppression in both chaparral and coastal sage scrub (Muller & Muller 1964; Muller et al. 1968). However, once herb cover in chaparral has been reduced for whatever reason, there will be fewer seeds locally to dis-

perse into bare areas, so that the relative absence of herbs from these areas cannot be taken as unequivocal evidence for inhibition.

The presence of potentially allelopathic substances in both chaparral and sage species has been established (Christensen & Muller 1975; Halligan 1973). The dramatic differences in herb cover between the two community types despite the abundance of allelopathic substances in both in itself suggests that factors other than allelopathy are playing major roles in inducing herb cover differences. The role of shading, rodents and other factors in inducing these differences has recently been reviewed (Mooney 1977; Westman 1979, 1981d). The critical importance of allelopathy in herb suppression has not yet been established.

Long-term viability of chaparral and sage scrub herb seeds has never been established (Went 1969; Westman 1979a). Since 58 percent of the immediate post-fire herbs in chaparral can be found in sage sites that have not burned in seven years or more, Westman (1979a) has suggested that post-fire herbs in chaparral seed in from adjacent coastal sage (and recently burned chaparral sites) every year, rather than remaining dormant in the soil for the many decades that can elapse between fires on a chaparral site. The seedlings only survive in the immediate post-fire chaparral environment, because of the abundance of light and nutrients or other factors. This suggests that coastal sage scrub is playing a role as repository for herbs that colonize chaparral after fire. A management implication is that, in order to assure native herb colonization of post-fire chaparral sites, one should not only ensure a mosaic of chaparral sites of various ages, but also preserve stands of coastal sage scrub that may be in the vicinity.

Shrub Reproduction

Westman et al. (1981) report that shrub seedling reproduction following fire in coastal sage scrub does not become common until the second year after fire. In the cases of *Encelia californica*, *Artemisia californica*, *Eriogonum cinereum* and *Yucca whipplei*, they observed crown-sprouting in the first year, and seedling reproduction only after these sprouts had flowered and set seed. In the case of *E. californica*, abundant seedling reproduction was visible a few cm. downslope of a resprout of the species which had set seed. This strongly suggests that shrub seeds on the site arise largely from "self-sowing" by crown sprouts following fire, rather than by survival of seeds through fire or by long-term seed dormancy. This conclusion is further strengthened by the slow return of shrub seedlings to River-sidian sites in which little or no crown sprouting is occurring (Westman et al. 1981).

Malanson and O'Leary (1981, in preparation) have further documented the relative reproduction by resprouts and by seeds at the end of the sec-

and year after fire on 7 sites including 4 reported earlier (Westman et al. 1981). Of 17 coastal sage shrub species encountered, all but *Eriogonum fasciculatum* and *Malacothamnus fasciculatus* showed substantially greater reestablishment of foliar cover by resprouting than seeding. Total foliar cover of resprouts exceeded that of seedlings by factors of 13 to 71 on the sites.

These studies leave little doubt that when fires do not kill root crowns, the main strategy for post-fire recovery in coastal sage scrub is by resprouting. In fact, the number of sage scrub species with the ability to resprout appears to exceed that of chaparral. Hanes (1971) reported that only 50 percent of the 59 shrubs in coastal chaparral are capable of resprouting. By contrast, of the 25 most widespread and dominant shrubs and small trees in coastal sage scrub, 100 percent of them show crown-sprouting ability, as do 28 percent of the herb species (Westman 1981d).

Earlier authors (e.g. Zedler 1977; Bradbury 1978; Kirkpatrick & Hutchinson 1980) have asserted that crown sprouting was not as common in coastal sage scrub as in chaparral. These observations may have arisen from the fact that there are sites of coastal sage scrub in which no crown-sprouting occurs following a particular fire, despite the presence of shrubs with the genetic potential to resprout (Westman et al. 1981). Westman et al. (1981) studied the relative roles that fire inten-

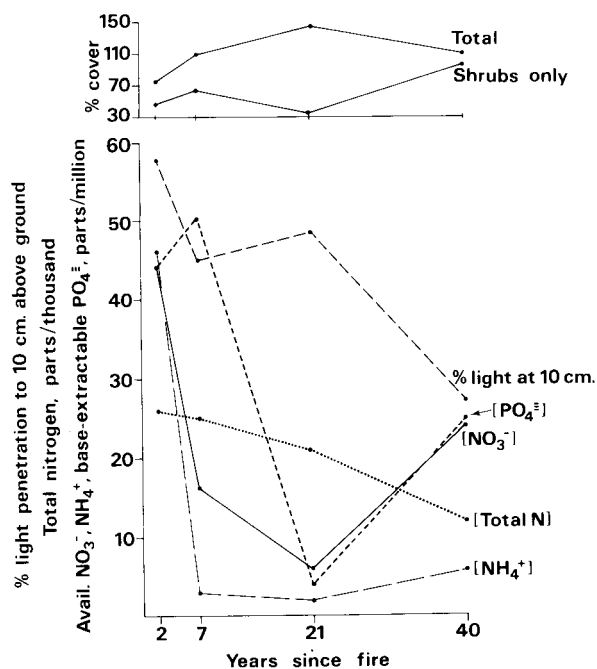


Figure 3. Trends in foliar cover, light penetration to herb level, and soil nutrient levels in four coastal sites of SW aspect, slope 7°-28°, in the Santa Monica Mountains (Los Angeles County). All substrates were shale, except the 7-year site, which was volcanic. The 21-year old site burned shortly after sampling and was resampled to provide the 2-year old site. Data from Westman 1981a, Westman et al. 1981 and Westman, unpublished.

sity, aspect, substrate and other factors might play in inducing this variability. They concluded that the potential vigor of resprouting is a genetic characteristic which varies widely from species to species, and possibly even among subspecies or ecotypes (e.g. Eriogonum fasciculatum). Thus a fire of lower intensity might be followed by less reprotouting than a site of higher intensity burn, if the species colonizing the former have lower heat tolerances and are inherently less vigorous reprotouters. Westman et al. (1981) provide a table of imputed tolerances of a range of coastal sage scrub species to fire intensity. It is possible that chaparral species capable of re-sprouting have a higher tolerance to fire intensity, but quantitative data on this point are lacking.

Age Structure

While chaparral seedlings cease to provide new recruits to the population after 5-10 years following fire, sage species are capable of continual seedling reproduction under their own canopy. Schlesinger & Gill (1978) document thinning in a chaparral stand of Ceanothus megacarpus in which there was apparently no seedling reproduction after the first year, and Hanes (1971) notes that seedling reproduction in chamise and mixed chaparral stands is only observable in the first decade after fire. By contrast, figure 2 shows the continual recruitment of individuals of Salvia mellifera to a Venturan coastal sage site in the 23 years after fire. Hanes (1971) similarly noted continual reproduction of sage species in openings in chaparral.

A significant implication of this difference in recruitment periods is that coastal sage scrub stands do not grow "senescent" as do chaparral stands of increasing age, because of the continual rejuvenation of the age structure in the former. Indeed, healthy stands of sage scrub occur which have not burned in 60 years or more, and in which the oldest dominant does not exceed 35 years in age (Westman 1981a). While allelopathy was suggested (Hanes 1971) as a cause of senescence in chaparral, this seems inadequate in view of the abundance of allelopathics in coastal sage scrub and the lack of senescence in its age structure. The failure of seedling survival, the tie-up of nitrogen in the aboveground parts, and the rising respiratory load of shrubs could provide an alternative explanation for chaparral senescence.

Differences in age structure between the community types also help us to understand why coastal sage and chaparral will occasionally maintain sharp, stable borders between them on a given hillside for many decades (e.g. Bradbury 1978). The sage shrubs, though shorter-lived, retain a healthy community through continual seedling reproduction. Sage seeds, while capable of germinating in the open canopy environment of sage scrub, are inhibited from growth under chaparral by shading (McPherson & Muller 1967). The chaparral, by contrast, produces seeds which typically germinate

only in the first few years after fire, for a variety of reasons: scarification requirements, nutrient deficiencies, herbivore grazing, possibly allelopathic inhibition (viz. Bradbury 1978; Christensen and Muller 1975; Hanes 1977 inter alia). The chaparral shrubs are longer-lived, however, and maintain an even-aged stand composed of the original post-fire shrubs, for many decades. In situations where climatic conditions or herbivore pressure prevent seedling establishment in the first year or two after fire, and re-establishment of vegetative canopies occur rapidly through crown sprouting, conditions would have obtained which would prevent either community type from invading the other in subsequent years.

Figure 3 shows trends in nitrogen, phosphorus and light penetration on coastal sage sites of different ages, on similar aspects, slopes and substrates. While total nitrogen does decline with age, available pools of N and P remain high at 15 cm depth even to age 40. This suggests that high rates of external nutrient cycling, and lower nutrient stocks in standing biomass, are responsible for maintenance of available nutrient pools in sage scrub. Still, with the decline in light penetration, seedling reproduction can be expected to decline with age, inducing some senescence in age structure, though not as severe as that in chaparral.

Experimental application of N and P to stands of Salvia mellifera of similar age range resulted in maximum shoot growth response to N alone or N with P, at age 25 (Davis 1980). The nitrogen response is not surprising in view of the lack of symbiotic N-fixers in coastal sage after age 20 (Westman 1981a). A similar shoot growth response to N has been found in chaparral (Hellmers et al. 1955a).

Fibrous Roots

Roots of coastal sage scrub species are, in general, shorter in both lateral and vertical spread than those of chaparral, and more fibrous (Hellmers et al. 1955b). Hellmers et al. (1955b) discussed the implications of this difference for surface soil erosion, mass slumping and water infiltration. The more fibrous roots of coastal sage apparently make them somewhat more efficient at capturing the early and light rains, and using this moisture for shoot growth (Harvey & Mooney 1964).

The microbial associates of the root systems are still poorly known. Symbiotic N-fixation occurs in some Ceanothus spp. (Kummerow et al. 1978), which persist in chaparral stands for at least 40 years. By contrast, the only substantial N-fixing symbiotic shrub species identified in coastal sage scrub is Lotus scoparius, which dies out within 20 years (Westman 1981a). Minor species of Lotus and Lupinus occur generally only in the first few years after fire, and do not produce significant biomass. Dunn & Poth (1979) report no asymbiotic N-fixation in chaparral soils during

the January-June period. The only known sources of initial N in coastal sage scrub at present, then, are a small amount of symbiotic N-fixation in the early post-fire years, and bulk precipitation. While nutrient recycling may be more rapid in sage, and uptake demand lower, the small sources of external N seem inadequate to balance the N budget; further research is needed on this point. A management implication, earlier drawn for chaparral, that fire temperatures be kept down to avoid N volatilization losses, and moist soils avoided during fire to avoid steam-killing of legume seeds (Dunn & Poth 1979), is even more critical to coastal sage scrub management.

Most coastal sage shrubs are believed to possess vascular-arbuscular mycorrhizae. The role these play in the plant nutrition of their hosts is unknown. Mycorrhizal associations are susceptible to air pollution damage (McCool & Menge 1978). Weeks and Westman are currently undertaking fumigation experiments to examine the effects of SO₂ and ozone on the endomycorrhizal associations of sage species.

CONCLUDING REMARKS

Analysis of the structural differences between coastal sage and chaparral permit an increased understanding of the differences in their successional processes. Malanson (1981, this volume) is currently working under Westman's supervision to produce a model of post-fire succession in coastal sage scrub based on the relative sprouting and seeding propensities of component species, scenarios of age-dependent natality and mortality rates, and models of interspecific competition. The underlying rationale for such a model is that succession in sage scrub is a process of scramble competition for resources following fire, in which crown sprouting vigor plays a key role. The model is in the tradition of the population-level analyses arising from the individualistic hypothesis (e.g. Whittaker & Levin 1977, Noble & Slatyer 1980).

Much remains to be learned about successional processes in coastal sage scrub. We already know that succession in coastal sage differs from that in chaparral in a number of respects. Herb growth after fire in sage scrub persists into the mature stands, where ground-level light continues to be abundant. Shrub dominants continue to reproduce by seed many decades after fire, maintaining healthy, mixed aged stands which may slow in growth rate and seedling reproduction only slightly after four decades or more. Crown-sprouting is even more important as a post-fire reproductive strategy among sage scrub dominants, but the vigor and heat-resistance of the sage species root crowns may be more variable than for chaparral.

For preservation of both root crowns and soil nitrogen levels, low-intensity fires are to be favored if rapid post-fire recovery is the goal. On the other hand, continued favoring of crown-sprouting will suppress the post-fire herb flora somewhat, and could lead to a gradual decline in

seeds for both chaparral and sage scrub post-fire herb communities in the long term.

The susceptibility of coastal sage scrub to air pollution damage (SO₂, possibly ozone) is greater than that for chaparral. Sage scrub species therefore make better biological monitors of the air pollution damage being suffered by southern California shrublands than do chaparral species.

Finally, it should be noted that much less acreage of coastal sage scrub than of chaparral is in preserve status. Coastal sage scrub is one of the most endangered habitats in California. Estimates of the extent of the former vegetation which has been cleared range from 36 to 85 percent for coastal sage (Klopatek et al. 1979; Westman 1981a) compared to 12 percent for chaparral (Klopatek et al. 1979). The samples that do exist are virtually all of the Venturan type. Increased efforts should be made to set aside areas of Riversidian and Diegan, as well as Venturan associations of coastal sage scrub, for the benefit of present and future generations.

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