Coastal Sage Scrub Succession[1]

Walter E. Westman[2]

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.

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 by 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

[2]Professor of Geography, University of California, Los Angeles, California 90024 USA

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 <u>Salvia</u>, <u>Encelia</u>, <u>Eriogonum</u> and <u>Artemisia</u>, 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. <u>Adenostoma</u> <u>fasciculatum</u>) 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; <u>Ceanothus</u> 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 SO_2 damage relative to sclerophyllous chaparral leaves. Suggestive evidence for damage to sage scrub in the field has been reported for SO_2 by Westman & Preston (1980) and for ozone by Westman (1979b). Preston and Westman are currently undertaking controlled fumigation experiments on sage species with SO_2 and ozone. A management implication is that sites of coastal sage make less desirable locations for siting of new pollution sources of SO_2 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 (<u>Eucalyptus</u> spp.: Rogers & Westman 1981), and data of Mooney and Kummerow (Mooney et al. 1977, Fig. 5-18, 5-19) suggest similar durations for <u>Heteromeles</u> <u>arbutifolia</u> and <u>Ceanothus</u> <u>leucodermis</u>. By contrast, mesophyllous sage scrub leaves invariably have shorter leaf durations (e.g. 30-50 days for <u>Artemisia</u> <u>californica</u>: 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 (<u>Aesculus</u> <u>parryi</u> and <u>A</u>. <u>californica</u> (Mooney & Bartholomew 1974); <u>Fraxinus</u> <u>trifoliata</u>; <u>Ptelea</u> <u>aptera</u>; <u>Prunus</u> <u>fremontii</u>) do show total seasonal deciduousness. Some of these (<u>F</u>. <u>trifoliata</u>, <u>Aesculus</u> 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 <u>Lotus</u> <u>scoparius</u>. 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 <u>Salvia</u> <u>leucophylla</u> and <u>S</u>. <u>mellifera</u>. 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 photoperi-odically, 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 adaptive-ness, 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, rela-tive to a 22-year-old pre-burn condition. It is possible that seasonal dimorphism provides a more effective post-fire recovery strategy on the bar-ren, 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 chap-arral. 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 postulat-ing a higher flammability for sage than chaparral species, all of which need further study: the high content (Tyson et al. 1974) and more wide-spread 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 ex-planation for it may be sought as a corollary to the Mutch (1970) fire-dependence hypothesis. Be-cause of a Mediterranean-type climate with a long dry season, but sufficient precipitation to sup-port 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 abund-ance of volatile, flammable oils in sage scrub than chaparral.

Indirect supporting evidence for this hypothe-sis comes from an analysis of fire frequency dur-ing 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 deter-mined. 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 oc-currences in the Western Santa Monica Mountains (K. Radtke, unpublished). Results indicate that fire frequencies are just as great in coastal sage as in chaparral ($\overline{X}$ occurrences for the 48-year period ± s.e.: 2.46 ± 0.11 for coastal sage scrub; 2.32 ± 0.15 for chamise-chaparral) despite lower fuel loads in the former. Mean fire inter-val 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 stand-ing, 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 implica-tions for succession. Firstly, the more rapid re-turn of dead wood to the litter layer provides im-proved nutrient turnover, and diminishes the chance for deficiencies in available nutrient stocks to develop, leading to the growth senes-cence reported for chaparral (Hanes 1971). A second implication is that dry fuel will be a
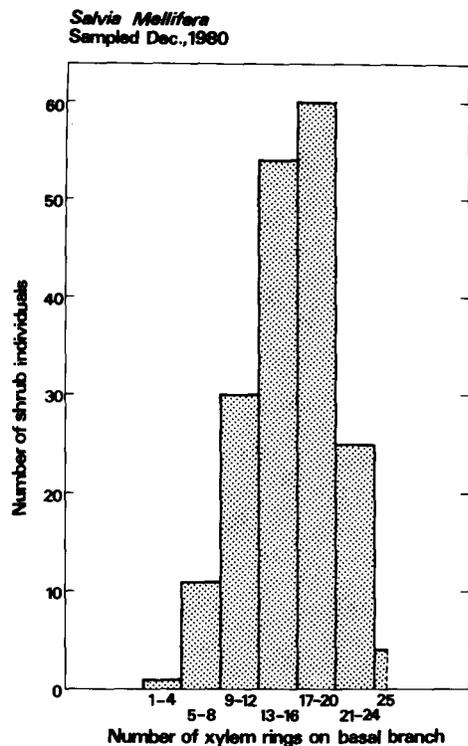
Figure 2. Numbers of individuals of Salvia melli-
fera showing a given number of xylem rings on the
lowest branch, on a 23-year-old coastal Venturan
site. Some individuals showed one or two extra
rings as a result of the production of double
rings in some years.

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 to-
tal 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 intensi-
ties were 170 - 200 kcal $sec^{-1}m^{-2}$; for Riversidian
types, 120 - 170 kcal $sec^{-1}m^{-2}$. These values are
low for the range of values modeled in fires in
older chaparral (up to 600 kcal $sec^{-1}m^{-2}$; Albini
1976b), but the latter are not field measurements.
Fire intensities clearly affect root crown survi-
val, 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, lit-
ter 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 Experi-
mental 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 con-
trast, 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 nutri-
ent contents (Mooney 1977) would inhibit leaf lit-
ter 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 ($\overline{X}$ = 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 immedi-
ately below the canopy of 200 - 900 microEinsteins
$m^2 sec^{-1}$ (Schlesinger & Gill 1980), two stands of
Venturan sage of 22 year age at Leo Carillo State
Park had mean irradiances of 900 - 1000 microEin-
steins $m^2 sec^{-1}$ 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 impor-
tant 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 sup-
pression in chaparral, since herbs are absent from
bare areas under canopy openings in mature chapar-
ral. He argues instead for the role of allelo-
pathic 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 respository 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 Riversidian 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 by 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-
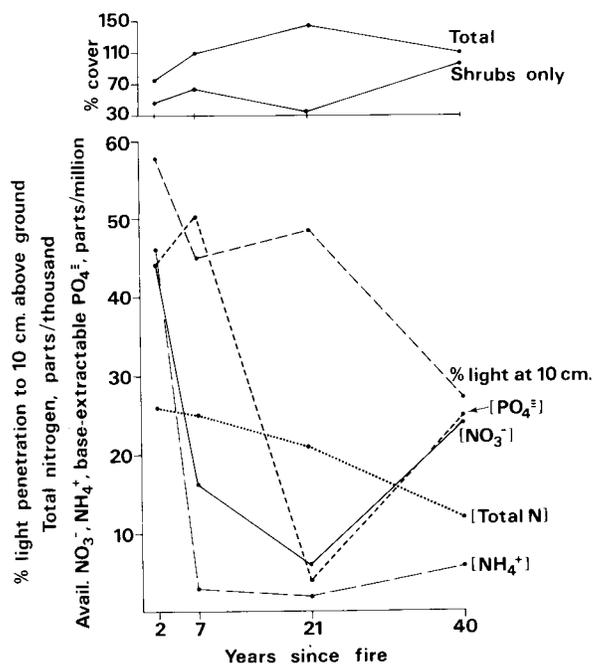

Figure 3. Trends in foliar cover, light penetration to herb level, and soil nutrient levels in four coastal sites of SW aspect, slope 7°-28°, in the Santa Monica Mountains (Los Angeles County). All substrates were shale, except the 7-year site, which was volcanic. The 21-year old site burned shortly 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 reprouting than a site of higher intensity burn, if the species colonizing the former have lower heat tolerances and are inherently less vigorous reprouters. 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 resprouting 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 reestablishment 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 SO_2 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 (SO_2, 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.

ACKNOWLEDGEMENTS

LITERATURE CITED

Albini, F.A. Computer-based models of wildland fire behavior: a user's manual. Ogden, Utah: Intermountain For. Range Exp. Stn., Forest Serv., U.S. Dep. Agric.: 1976a; 68 p.

Albini, F.A. Estimating wildfire behavior and effects. Forest Serv., U.S. Dep. Agric.: 1976b, Gen. Tech. Rep. INT-30.

Axelrod, D.A. The origin of coastal sage vegetation, Alta and Baja California. Amer. J. Bot. 65: 1117-1131, 1978.

Bradbury, D.E. The evolution and persistence of a local sage/chamise community pattern in southern California. Yearbook Assoc. Pacif. Coast Geographers 40: 39-56, 1978.

Christensen, N.L.; Muller, C.H. Relative importance of factors controlling germination and seedling survival in Adenostoma chaparral. Amer. Midl. Nat. 93: 71-78, 1975.

Cunningham, G.L.; Strain, B.R. An ecological significance of seasonal leaf variability in a desert shrub. Ecology 50: 400-408, 1969.

Davis, Z.W. The effects of applied nutrients on Salvia mellifera (black sage) stands of different ages. M.A. thesis, Univ. Calif., Los Angeles, 1980.

Dunn, P.H.; Poth, M. Nitrogen replacement after fire in chaparral. In: Gordon, J.C.; Wheeler, C.T.; Perry, D.A., eds., Symbiotic Nitrogen Fixation in the Management of Temperate Forests. Corvallis, Ore.: Forest Res. Lab., Oregon State Univ., 1979: 287-293.

Gaff, D.F. Desiccation-tolerant flowering plants in southern Africa. Science 174: 1033-1034. 1971

Gaff, D.F.; Churchill, D.M. _Borya nitida_ Labill.: An Australian species in the Liliaceae with desiccation-tolerant leaves. Aust. J. Bot. 24: 209-224; 1976.

Gray, J.T.; Schlesinger, W.H. Biomass, production, and litterfall in the coastal sage scrub of southern California. Amer. J. Bot. 68: 24-33; 1981.

Halligan, J.P. Bare areas associated with shrub stands in grassland: the case of _Artemisia californica._ BioScience 23: 429-432; 1973.

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

Hanes, T.L. Chaparral. _In_: Barbour, M.; Major, J., eds. Terrestrial Vegetation of California. New York: J. Wiley; 1977: 417-470.

Harrison, A.; Small, E.; Mooney, H.A. Drought relationships and distribution of two mediterranean climate California plant communities. Ecology 52; 869-875; 1971.

Harvey, R.; Mooney, H.A. Extended dormancy of chaparral shrubs during severe drought. Madroño 17: 161-165; 1964.

Heady, H.F.; Foin, T.C.; Hektner, M.M., Taylor, D.W.; Barbour, M.G.; Barry, W.J. Coastal prairie and northern coastal scrub. _In_: Barbour, M.G.; Major, J. eds. Terrestrial Vegetation of California. New York: J. Wiley; 1977; 733-762.

Hellmers, H.; Bonner, J.; Kelleher, J.M. Soil fertility: a watershed management problem in the San Gabriel mountains of southern California. Soil Science 80: 189-197; 1955a.

Hellmers, H.; Horton, J.S.; Juhren, G.; O'Keefe, Root systems of some chaparral plants in southern California. Ecology 36: 667-668; 1955b.

Horton, J.S.; Kraebel, J.C. Development of vegetation after fire in the chamise chaparral of southern California. Ecology 36: 244-262; 1955.

Kirkpatrick, J.B.; Hutchinson, C.F. The community composition of Californian coastal sage scrub. Vegetatio 35: 21-33; 1977.

Kittredge, J. Litter and forest floor of the chaparral in parts of the San Dimas experimental forest, California. Hilgardia 23: 563-596; 1955.

Klopatek, J.M.; Olson, R.J.; Emerson, C.J.; Joness, J.L. Land-use conflicts with natural vegetation in the United States. Envir. Conserv. 6: 191-199; 1979.

Kummerow, J.; Alexander, J.V.; Neel, J.W.; Fishbeck, Symbiotic nitrogen fixation in _Ceanothus_ roots. Amer. J. Bot. 65: 63-69; 1978.

Margaris, N.S. Effect of photoperiod on seasonal dimorphism of some mediterranean plants. Ber. Schweiz. Bot. Ges. 85: 96-102; 1975.

McCool, P.M.; Menge, J.A. Interaction of air pollutants and mycorrhizae. California Air Envir. 7: 1,2,4; 1978.

McPherson, J.K.; Muller, C.H. Light competition between _Ceanothus_ and _Salvia_ shrubs. Bull. Torrey Bot. Club 94: 41-55; 1967.

McPherson, J.K.; Muller, C.H. Allelopathic effect of _Adenostoma fasciculatum_, "chamise", in the California chaparral. Ecol. Monogr. 39: 177-198; 1969.

Montenegro, G.; Aljaro, M.E.; Kummerow, J. Growth dynamics of-Chilean mattoral shrubs. Bot. Gaz. 140: 114-119; 1979a.

Montenegro, G.; Hoffman, A.J.; Aljaro, M.E.; Hoffman, A.E. _Satureja gilliesii_, a poikilohydric shrub from the Chilean mediterranean vegetation. Can. J. Bot. 57: 1206-1213; 1969b.

Mooney, H.A. Southern coastal scrub. _In_: Barbour, M.; Major, J., eds. Terrestrial Vegetation of California. New York: J. Wiley; 1977; 471-490.

Mooney, H.A.; Bartholomew, B. Carbon balance of two Californian _Aesculus_ species. Bot. Gaz. 135: 306-313; 1974.

Mooney, H.A.; Kummerow, J.; Chu, C.; Hays, R.I. Biomass, energy and mineral characteristics. _In_: Thrower, N.J.W.; Bradbury, D.E., eds. Chile-California Mediterranean Scrub Atlas. A Comparative Analysis. Stroudsberg, Pa.: Dowden, Hutchinson & Ross; 1977a; 162-164.

Mooney, H.A.; Kummerow, J.; Johnson, A.W.; Parsons, D.J.; Keeley, S.; Hoffman, A.; Hays, R.I.; Giliberto, J.; Chu, C. The producers -- their resources and adaptive responses. _In_: Mooney, H.A., ed. Convergent Evolution in Chile and California Mediterranean Climate Ecosystems. Stroudsberg, Pa.: Dowden, Hutchinson & Ross; 1977b; 85-143.

Mooney, H.A.; Harrison, A. The vegetation gradient on the lower slopes of the Sierra San Pedro Martir in northwest Baja California. Madroño 21: 439-445; 1972.

Mooney, H.A.; Rundel, P.W. Nutrient relations of the evergreen shrub, _Adenostoma fasciculatum_, in the California chaparral. Bot. Gaz. 140: 109-113; 1979.

Muller, C.H.; Hanawalt, R.B.; McPherson, J.K. Allelopathic control of herb growth in the fire cycle of California chaparral. Bull. Torrey Bot. Club 95: 225-231; 1968.

Muller, W.H.; Muller, C.H. Volatile growth inhibitors produced by _Salvia_ species. Bull. Torrey Bot. Club 91: 327-330; 1964.

Mutch, R.W. Wildland fires and ecosystems -- a hypothesis. Ecology 51: 1046-1051; 1970.

Nilsen, E.T.; Muller, W.H. An evaluation of summer deciduousness in _Lotus scoparius_ Nutt. (T.&G.). Amer. Midl. Nat. 103: 88-95; 1980.

Noble, I.R.; Slatyer, R.O. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5-21; 1980.

Orshan, G. Seasonal dimorphism of desert and Mediterranean chamaephytes and its significance as a factor in their water economy. _In_: Rutter, A.J.; Whitehead, R.H., eds. The Water Relations of Plants. Oxford: Blackwell Sci. Publ.; 1963; 206-222.

Philbrick, R.N.; Haller, J.R. The southern California islands. _In_: Barbour, M.; Major, J., eds. Terrestrial Vegetation of California. New York: J. Wiley; 1977; 893-908.

Rogers, R.W.; Westman, W.E. Growth rhythms and productivity of a coastal subtropical eucalypt forest. Aust. J. Ecol. 6(1): in press; 1981.

Sampson, A.W. Plant succession on burned chaparral lands in northern California. Calif. Agr. Exp. Sta.: 1944; Bull. 685. 144 p.

Schlesinger, W.H.; Gill, D.S. Demographic studies of the chaparral shrub, _Ceanothus megacarpus_,

in the Santa Ynez Mountains, California. Ecology 59: 1256-1265; 1978.

Schlesinger, W.H.; Gill, D.S. Biomass, production, and changes in the availability of light, water, and nutrients during the development of pure stands of the chaparral shrub, Ceanothus megacarpus, after fire. Ecology 61: 781-789; 1980.

Smith, W.K.; Nobel, P.S. Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. Ecology 58: 1033-1043; 1977.

Tyson, B.J.; Dement, W.A.; Mooney, H.A. Volatilisation of terpenes from Salvia mellifera. Nature 252: 119-120; 1974.

Went, F.W. A long term test of seed longevity. II. Aliso 7: 1-12; 1969.

Westman, W.E. A potential role of coastal sage scrub understories in the recovery of chaparral after fire. Madroño 26: 64-68; 1979a.

Westman, W.E. Oxidant effects on Californian coastal sage scrub. Science 205: 1001-1003; 1979b.

Westman, W.E. Diversity relations and succession in Californian coastal sage scrub. Ecology 62: 170-184; 1981a.

Westman, W.E. Factors influencing the distribution of species of Californian coastal sage scrub. Ecology 62: in press; 1981b.

Westman, W.E. Seasonal dimorphism of foliage in Californian coastal sage scrub. Oecologia: submitted; 1981c.

Westman, W.E. Plant community structure -- spatial partitioning of resources. In: Kruger, F.J.; Mitchell, D.T.; Jarvis, J.U.M., eds. Mediterranean-type Ecosystems. The Role of Nutrients. Berlin-Heidelberg-New York: Springer-Verlag; In press; 1981d.

Westman, W.E.; O'Leary, J.F.; Malanson, G.P. The effects of fire intensity, aspect and substrate on post-fire growth of Californian coastal sage scrub. In: Margaris, N.S.; Mooney, H.A., eds. Components of Productivity of Mediterranean regions -- Basic and applied aspects. The Hague: W. Junk. In press; 1981.

Westman, W.E.; Preston, K.P. Sulfur dioxide and oxidant effects of Californian coastal sage scrub. In: Proc. Symp. Effects of Air Pollutants on Mediterranean and Temperate Forest Ecosystems. Berkeley, Calif.: U.S. Dep. Agric.: 1981; Forest Serv. Gen. Tech. Rep. PSW-43.: 256.

Whittaker, R.H. Communities and Ecosystems. New York: Macmillan; 1970.

Whittaker, R.H.; Levin, S.A. The role of mosaic phenomena in natural communities. Theor. Pop. Biol. 12: 117-139; 1977.

Winner, W.A.; Mooney, H.A. Ecology of SO_2 resistance: II. Photosynethic changes of shrubs in relation to SO2 absorption and stomatal behavior. Oecologia 44: 296-302; 1980.

Zedler, P.H. Life history attributes of plants and the fire cycle: a case study in chaparral dominated by Cupressus forbesii. In: Proc. Symp. Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems. Washington, D.C.: U.S. Dep. Agric.: 1977; Forest Serv., Gen. Tech. Rep. WO-3: 451-458.