HISTORICAL DECLINE OF COASTAL SAGE SCRUB IN THE RIVERSIDE–PERRIS PLAIN, CALIFORNIA

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Californian coastal sage scrub (CSS), which consists of dense stands of soft-leaved drought-deciduous subshrubs 0.5–1.5 m tall, has been extensively cleared for agriculture and urbanization (Westman 1981). The state of California has initiated a regionally focused conservation-planning process for natural communities, including CSS, in southern California (O'Leary et al. 1992). To protect two endangered species of CSS, the Stephens' Kangaroo Rat (*Dipodomys stephensi*) and the California Gnatcatcher (*Polioptila californica*), Riverside County has developed a habitat-conservation plan for CSS in the Riverside–Perris Plain, an area of rapid present and future urbanization. This has resulted in protection of CSS through purchase of private lands surrounding preexisting public lands, largely through political and economic incentives (Feldman 1995).

Few studies have examined the landscape-scale dynamics of surviving CSS, particularly in relation to the invasion of exotic annuals introduced from the Mediterranean basin and Middle East since the late 18th century. While it is widely reported that exotic annuals have displaced indigenous herbaceous ecosystems (McNaughton 1968, Gulmon 1977, Heady 1988, Drake and Mooney 1986, Huenneke et al. 1990, D'Antonio and Vitousek 1992), relationships between the spread of these annuals and the dynamics of shrubland communities are not well understood. O'Leary and Westman (1988) and O'Leary (1990) demonstrated that CSS has been reduced by frequent fire, grazing, and the invasion of exotic annuals, as well as air pollution. These trends have special importance for the endangered California Gnatcatcher, whose habitat requirements include dense stands of CSS with high shrub-species diversity (Atwood 1993). Planning efforts have not taken into account whether CSS is a static system.

From 1929 to 1934 the vegetation of California was inventoried by the Vegetation Type Map (VTM) Survey under the California Forest and Range Experiment Station (Minnich et al. 1995). During the survey, 78 plots of CSS were surveyed in the Riverside–Perris Plain. The objective of our study is to replicate the VTM for this area to quantify change of CSS over the past 60 years and to evaluate the role of exotics, specifically, whether the invasion of exotics is dependent on frequent burning or whether exotics promote frequent burning. The answer to this question affects whether management should focus on disturbance or the control of exotics. Addressing the question requires the examination of such processes associated in habitat change, including disturbance, grazing, competitive replacement, and air pollution.

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STUDY AREA

The Riverside–Perris Plain is a fault-bound alluvial basin with scattered small hills (elevation 600–1000 m) 80 km east of Los Angeles, California (Figure 1). Although the floor of the plain has been largely cultivated since ca. 1900, hillsides are covered with CSS dominated by *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia mellifera*, *S. apiana*, and *Encelia farinosa* (plant names after Hickman 1993). The climate is Mediterranean with winter rain from frontal cyclones and summer drought. The rain shadow of the Santa Ana Mountains to the west leaves the plain with mean annual precipitation of 25 to 30 cm, falling mostly between November and April. The Santa Ana Mountains also isolate the basin from cooling sea breezes, resulting in maximum temperatures >35°C from June to September.

METHODS

We mapped CSS in the Riverside–Perris Plain from Kodak Type 2443 color positive transparencies taken from an aircraft in 1990 (scale 1:20,000), using a roll-film stereoscope with 3 and 8× magnification and a standard pocket stereoscope. CSS is recognized from the blue-gray color and low stature of subshrubs. We identified three types on the basis of cover: (1) dense coastal sage scrub (subshrubs forming contiguous stands), (2) mixed coastal sage scrub/exotic grassland (open stands of subshrubs with understory of exotic annuals), and (3) exotic grasslands (continuous exotic annuals

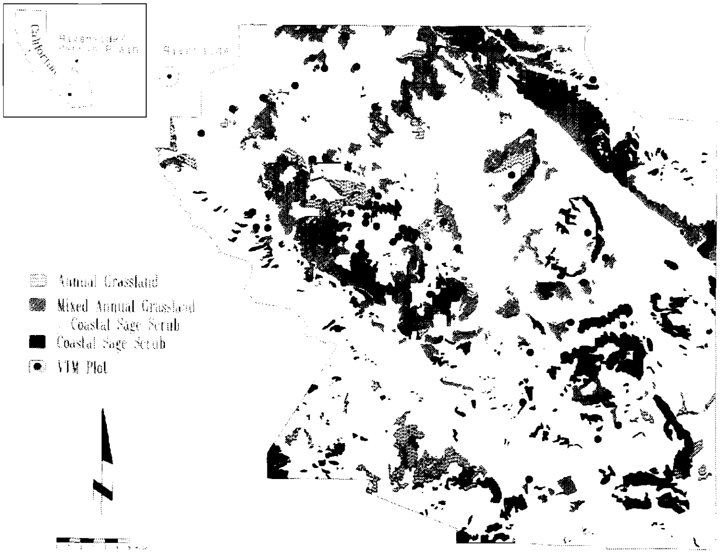


Figure 1. Coastal sage scrub in the Riverside–Perris Plain, with locations of California Vegetation Type Maps (VTM) plots.

with subshrub cover <20%). Boundary data were transferred onto 1:24,000 topographic sheets by means of a zoom transfer scope. The vegetation map and VTM data were entered into the Arc-Info geographic-information system installed on a Sun workstation. General methods are given in Minnich (1987).

We compiled data from VTM plots from original records. The plots consist of 20 field quadrats covering 0.005 acres (0.04 ha, on file at the Department of Environmental Science, Policy, and Management, University of California, Berkeley). Although VTM workers did not leave permanent markers, we believe that plots could be relocated within a radius of 100 m from localities given on manuscript maps (Minnich et al. 1995). We sampled each site three times, subjectively scattering replicate plots over an area of 1.0 ha, with each matching the slope and aspect conditions given on original field sheets. The three replicates were averaged to achieve one modern composite sample to be compared with original data. In each plot the dominant shrub species is identified for each 0.001 acre (ca. 2 m^2). No species are recorded for individual quadrats lacking shrub cover. Eighty-two plots were visited in 1930, but four had been cleared for urbanization or fuelbreaks, leaving a total sample of 78 plots. Some change between 1930 and 1992 may be due to sampling error in relocation, but we believe that actual changes will emerge as a result of the large sample size.

RESULTS

Published VTM vegetation maps (Riverside, San Jacinto quadrangles; Weislander 1934, 1938) show that CSS covered ca. 74,950 ha, concentrated on hilly terrain of the Riverside–Perris Plain. Most stands were apparently dense, as only a few hills were shown as "semibarren." This is confirmed by aerial photographs taken in 1931, 1948, 1952, and 1962 (on file, Riverside County Department of Public Works). VTM field sheets disclose that most semibarren sites were recently burned. A few sites are too rocky to support dense cover. VTM vegetation maps give a hierarchical classification by life-form and species dominance (species ±20% cover). In the northern Riverside–Perris Plain, stands were dominated by *Encelia farinosa* on southern exposures, *Eriogonum fasciculatum* and *Artemisia californica* on northern exposures. Farther south, most stands comprised mixtures of *Eriogonum fasciculatum*, *Artemisia californica*, and *Salvia mellifera*. Monotypic stands of *Eriogonum fasciculatum* covered hillsides in the far south. *Salvia mellifera* was dominant in the Santa Ana Mountains and the badlands of the northeast. Other stands of *S. mellifera* were found in the central Riverside–Perris Plain in association with underlying Mesozoic basic intrusive rocks (gabbro basalts, Calif. Div. Mines 1969).

By 1990, only 30,118 ha or 40.1% of the stands mapped as CSS by VTM workers still existed as contiguous stands (Figure 1), with most occurring on outcrops of Mesozoic gabbro basalts in the south. Another 31,408 ha (41.9% of stands) were open CSS mixed with a continuous layer of exotic annual grasses. The remaining 13,424 ha (18.0%) were entirely converted to exotic grassland, with most conversions concentrated in valley edges and north-facing slopes. Cursory field observations indicate that pure exotic grasslands and exotic grasslands mixed with CSS are dominated by *Bromus madritensis* ssp. *rubens* on southern exposures and *B. diandrus* on northern exposures. Other important species include *Avena barbata*, *Brassica geniculata*, *Schismus barbatus*, and *Erodium cicutarium*. *Brassica tournefortii*, native to the Sahara Desert, was introduced into the southern California deserts in 1927 and began invading hillsides near Riverside about 1987 (Minnich and Sanders in press). Time-series ground photographs in Riverside show that CSS declined largely after the 1950s (Figure 2).

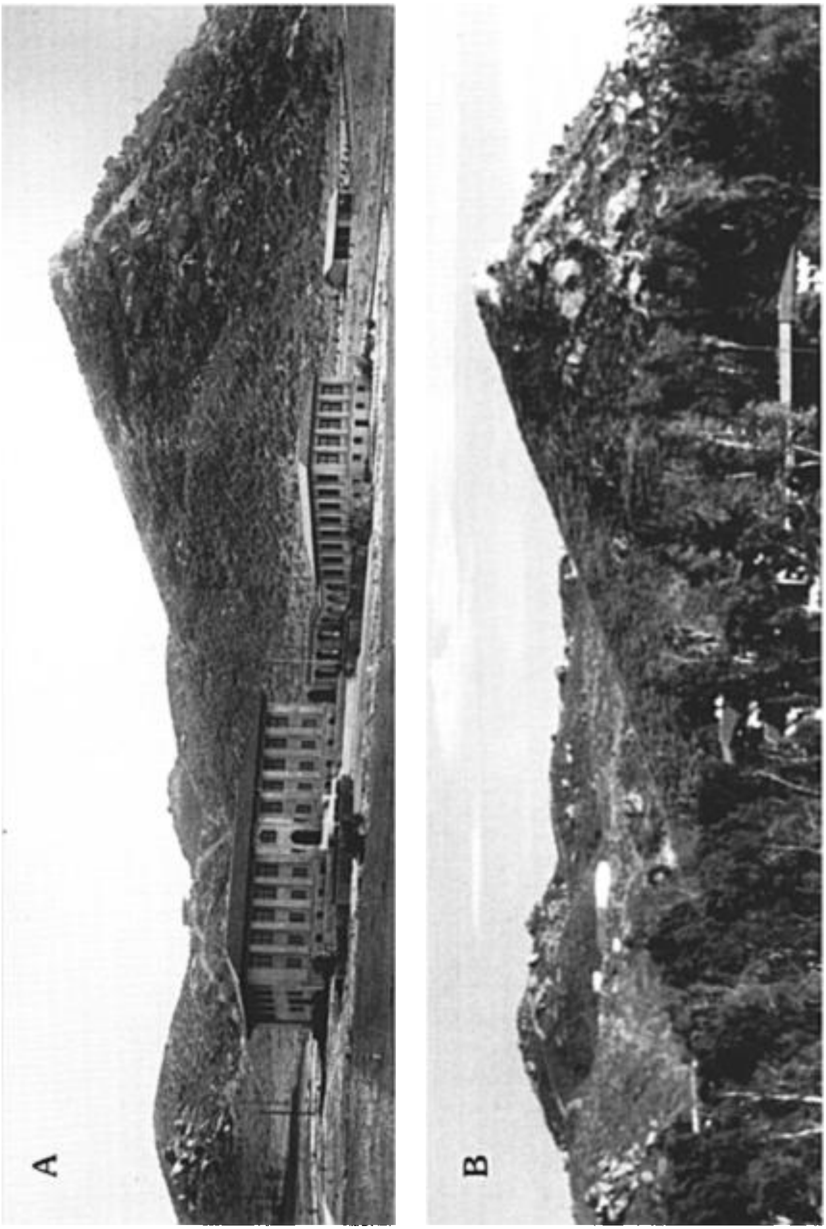
Replicates of VTM plots revealed significant changes in shrub cover and species composition (Figure 3). VTM workers recorded 60 to 90% shrub cover at most sites. Field sheets show that three plots with <40% were each burned during the late 1920s. Most plots had two or three species with at least 20% cover, although some were dominated by one species, usually *Artemisia californica* on north-facing slopes, *Eriogonum fasciculatum* on flats or steep bluffs, *Encelia farinosa* on south-facing slopes in the north, or *Salvia mellifera* on gabbro basalts. Other species frequently recorded on VTM plots include *Lotus scoparius*, *Keckiella antirrhinoides*, *Malacothamnus fasciculata*, *Opuntia littoralis,* and *Bebbia juncea*.

Our replicates showed that shrub cover had declined to an average of 36% (Figure 3) and that dominance was usually restricted to a single species, according to VTM criteria. Plots with <30% shrub cover frequently had no dominant species. The cover of *Salvia apiana* decreased from 7.4 to 1.7%, that of *S. mellifera* from 13.9 to 6.1%, that of *Artemisia californica* from 17.7 to 6.1%, that of *Eriogonum fasciculatum* from 20.2 to 9.0%. Average cover of *Encelia farinosa* increased from 4.6 to 5.2%.

The change in total shrub cover varied greatly from site to site, ranging from stability (<5% losses) to total displacement of dense cover by annual grassland (>90% losses, Figure 4). Modal shrub loss was 40%. Among dominant species, *Artemisia californica* experienced the greatest loss, although on many plots its decline was <20%. Modal loss was 10–30% for all species except *Encelia farinosa*. The frequency of plots with shrub losses was far greater than of plots with gains.

Total shrub cover declined on most substrates (Figure 5). Modal declines were 50% on granitoid rocks and Pauba (Pliocene) and Pleistocene sandstones, 30–60% on Santiago Peak volcanics and the Jurassic Bedford Formation, 20% on gabbro basalts. The greatest losses were of *Artemisia californica* and *Eriogonum fasciculatum* on alluvium and *Salvia mellifera*, *Artemisia californica*, and *Eriogonum fasciculatum* on Santiago Peak volcanics and the Jurassic Bedford Formation. All species except *Encelia farinosa* experienced at least a 10% decline on granitoid rocks. Shrub losses have resulted in shifts in species composition on various rock units (Table 1). *Eriogonum fasciculatum* is no longer dominant on granitoid rocks, while on Santiago Peak volcanics and the Jurassic Bedford Formation *Artemisia californica/Eriogonum fasciculatum* codominance has shifted to monotypic dominance of *Eriogonum fasciculatum*. *Encelia farinosa* experienced relative gains to other species on all rock units.

The magnitude of total shrub loss correlates with the decline of individual species (Table 2). Plots with >35% cover losses are typically associated with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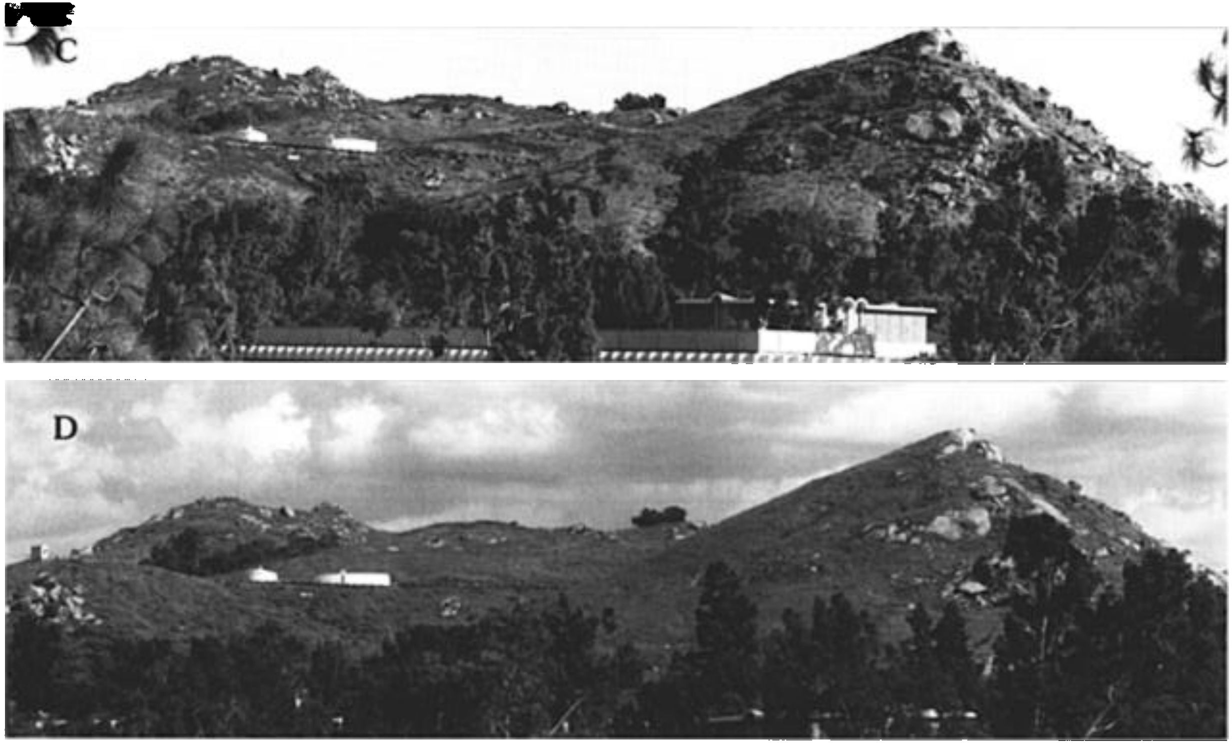

Figure 2. Coastal sage scrub on Picnic Hill, on the campus of the University of California, Riverside. A, 1917. Dense shrub cover of various sizes and shapes suggests a diverse species composition, mostly of *Artemisia californica*, *Eriogonum fasciculatum*, and *Salvia apiana*. Exotic annuals are absent. B, 1954. Contiguous shrub cover with comparable species diversity. C, 1992. Open stands surrounded by exotic annual grassland (mostly *Bromus diandrus*). Hill with water tank has small patches of *Encelia farinosa* on south-facing exposures. D, 1998. Dense cover of exotic grassland, the remaining shrubs having burned in a fire two years before. Patches of *Encelia farinosa* survive near the water tank.

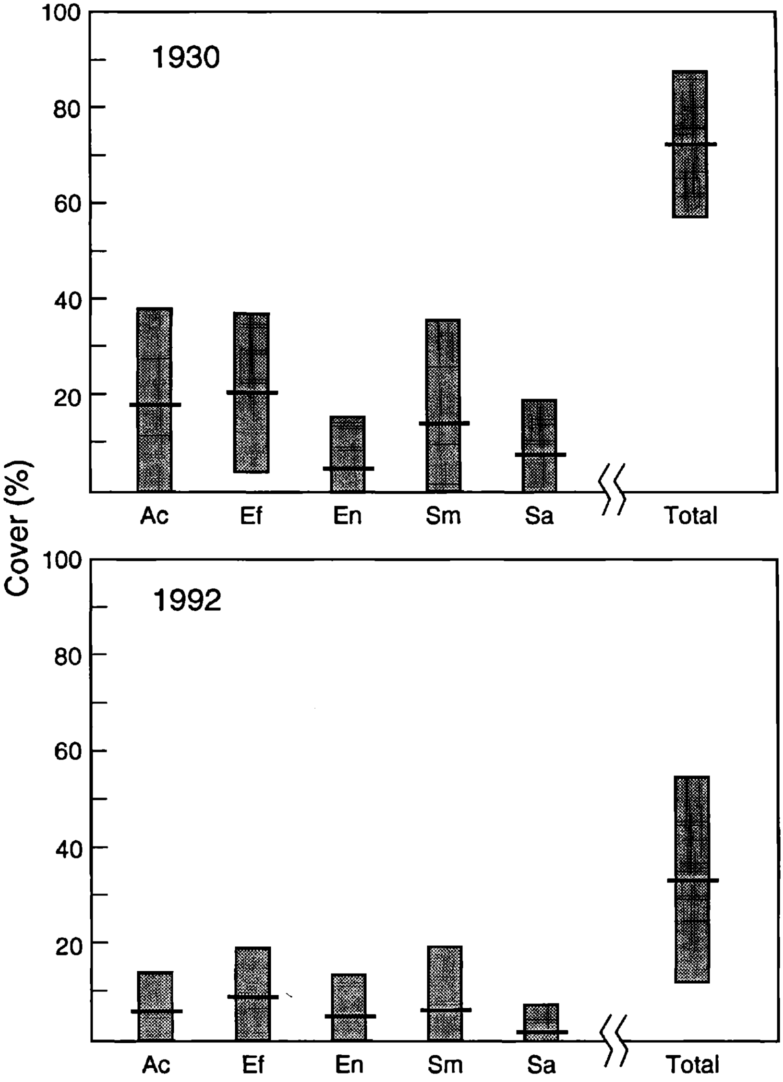

Figure 3. Cover of coastal sage scrub in the Riverside–Perris Plain in 1930 and 1992.

large declines in *Artemisia californica* and *Eriogonum fasciculatum* and virtual disappearance of *Salvia apiana* and *S. mellifera*. *S. mellifera* was stable only in plots with <35% decline. All species except *S. apiana* were stable in plots having declines of <15%. *Encelia farinosa* was stable at all rates of stand-thinning.

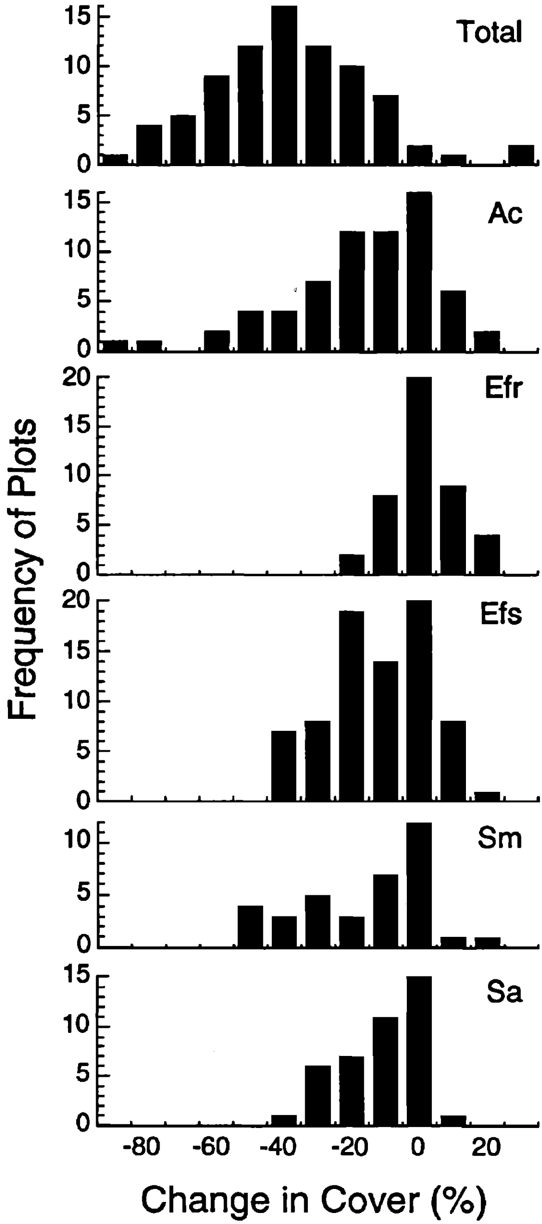

Figure 4. Change in cover by species. Ac, *Artemisia californica*; Efr, *Encelia farinosa*; Efs, *Eriogonum fasciculatum*; Sa, *Salvia apiana*; Sm, *Salvia mellifera*.

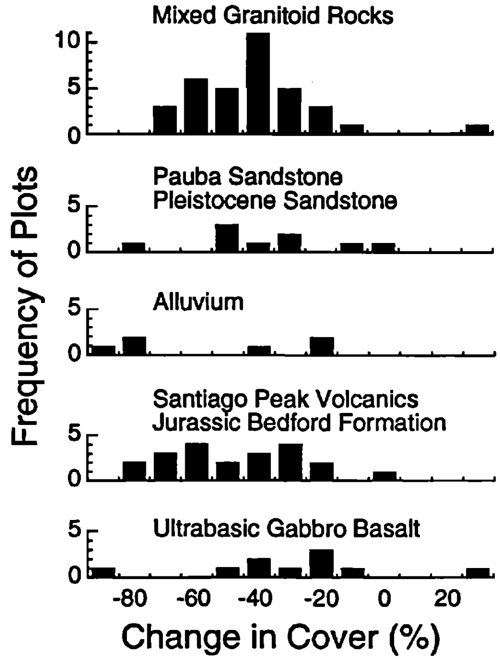

Figure 5. Change in cover of coastal sage scrub by substrate (Calif. Div. Mines 1969).

The majority of VTM plots had burned within the previous 20 years. Chronosequences of plot replicates show that average shrub cover increased from 22% for 0–9 years after a fire to 48% for 30–39 years afterward (Figure 6). Stands last burned >40 years ago still had lower average cover (31%) than recorded in the original VTM survey. Postfire species composition compared against VTM data appears to be uniform through time, as all species seem to reestablish themselves early in succession (Table 3). *Encelia farinosa* reached mature cover in 10 years, *Artemisia californica* and *Salvia apiana* approached half of VTM values only after 20 years, *Eriogonum fasciculatum* reached VTM values in 20 to 40 years, and dense *Salvia mellifera* stands were found primarily in areas last burned >40 years ago.

Although stand-thinning may lead to a decline in shrub diversity, the numbers of species recorded in plot replicates are similar to those during the original survey, with two to five dominants occurring in 71% of plots in 1932, in 68% of plots in 1992. The cover of extirpated species reported in 1932, however, was consistently greater than for immigrating species seen today. The patterns of immigrations and extinctions vary by species (Table 4). *Artemisia californica* immigrated into more sites than it was extirpated from, but sites of extirpation had 42% cover in 1932 while immigrants produced only 5% cover in 1992. *Eriogonum fasciculatum* and *Salvia mellifera* were

Table 1 Change in Average Shrub Cover in the Riverside–Perris Plain by Substrate

	Cover by species (%)					
Substrate	*Artemisia californica*	*Encelia farinosa*	*Eriogonum fasciculatum*	*Salvia apiana*	*Salvia mellifera*	*n*
Quaternary alluvium						
1932	32.2	0.1	22.8	5.6	0	8
	(15.5)[a]	(0.3)	(4.9)	(8.1)	–	
1992	10.5	2.5	9.0	1.8	0	
	(9.8)	(6.2)	(10.1)	(3.4)	–	
Undivided Pliocene nonmarine sedimentary						
1932	20.0	5.7	17.5	1.0	30.0	6
	(28.1)	(8.8)	(21.2)	(2.2)	(23.1)	
1992	7.8	3.7	6.8	0	5.5	
	(13.6)	(6.9)	(12.8)	–	(8.0)	
Jurassic marine and metavolcanic						
1932	21.7	5.9	21.7	11.2	4.9	21
	(19.5)	(13.2)	(15.7)	(12.5)	(8.5)	
1992	5.1	7.0	9.4	4.9	2.2	
	(5.8)	(10.9)	(9.6)	(10.4)	(5.5)	
Mesozoic basic intrusive						
1932	11.9	0	17.9	3.5	38.6	10
	(17.9)	–	(13.0)	(8.4)	(25.8)	
1992	8.1	1.2	14.1	0.1	30.6	
	(7.8)	(3.6)	(12.8)	(0.3)	(21.6)	
Granitoid						
1932	15.7	6.9	22.8	8.9	11.6	32
	(18.4)	(11.8)	(16.9)	(12.1)	(20.7)	
1992	5.6	7.1	8.3	0.7	2.8	
	(6.5)	(10.3)	(8.7)	(1.5)	(6.4)	

[a] Standard deviations in parentheses.

extirpated at twice as many sites as they immigrated to, and the 1932 cover of extirpated populations was twice that of 1992 immigrant populations. *S. apiana* died out at 42% of the original VTM plots, and new populations developed at only three localities. For *Encelia farinosa*, local immigrations were greater than extirpations, with an average cover of 5% for each.

Twenty-two plots (28.2% of the sample) had at least 10% cover of dead mature shrubs. High mortality was most common in plots last burned <40 years ago but also occurred in plots in early postfire succession (data not shown).

DISCUSSION

Replication of 78 VTM quadrats in the Riverside–Perris Plain reveals significant stand-thinning over the past 60 years. At many sites, formerly dense shrub cover became open with a continuous layer of exotic annuals dominated by either *Bromus diandrus* or *B. madritensis*. Among dominant

Table 2 Change in Average Cover by Species in the Riverside–Perris Plain Compared with Change in Total Shrub Cover

		Cover by species (%)					
Change in total shrub cover (%)	Year	*Artemisia californica*	*Encelia farinosa*	*Eriogonum fasciculatum*	*Salvia apiana*	*Salvia mellifera*	*n*
<-55	1932	26.3	3.9	23.3	10.9	12.8	18
		(26.5)[a]	(7.2)	(16.3)	(11.8)	(21.8)	
	1992	3.3	4.4	2.8	0.6	0.5	
		(4.3)	(9.1)	(4.2)	(1.4)	(1.2)	
-35 to -55	1932	23.1	6.0	17.7	6.0	13.7	27
		(19.1)	(12.4)	(16.4)	(9.8)	(20.3)	
	1992	6.5	7.5	7.3	1.0	3.2	
		(6.2)	(9.7)	(7.7)	(1.8)	(5.2)	
-15 to -35	1932	11.9	7.0	27.7	8.2	7.1	21
		(12.0)	(13.3)	(14.3)	(15.5)	(16.2)	
	1992	7.0	6.3	13.7	1.3	6.4	
		(9.6)	(11.0)	(11.5)	(2.8)	(12.1)	
>-15	1932	9.8	1.1	16.3	10.1	20.9	12
		(13.7)	(3.1)	(9.9)	(13.6)	(25.8)	
	1992	10.3	2.2	23.2	6.2	18.3	
		(9.8)	(4.9)	(14.7)	(13.4)	(21.3)	

[a] Standard deviations in parentheses.

shrubs, only *Encelia farinosa* has been stable, while *Eriogonum fasciculatum*, *Salvia apiana*, *S. mellifera*, and *Artemisia californica* have decreased since the original survey. *Artemisia californica* experienced the greatest losses, perhaps because it was abundant on north-facing slopes now densely covered with exotic annual grassland. The decline of *Eriogonum fasciculatum* appears to be moderated by the high diversity of habitats it occupies, including flats and cliffs, where exotics are discouraged. *Salvia mellifera* losses were large except on gabbro basalts, and *S. apiana* has experienced both widespread declines and local extirpations. Dense CSS now persists mostly on steep, rocky slopes too porous for the establishment of annuals and on gabbro basalts (Figure 1).

Other broad-scale surveys of vegetation change in CSS give mixed results. From aerial photographs repeated in 1947 and 1989 near Santa Barbara, Callaway and Davis (1993) found that grassland was converted to coastal sage scrub but that *Quercus agrifolia* woodland was converted to grassland in the absence of fire because of suppression of the shrub layer. O'Leary and Westman (1988) found that CSS was more resilient under periodic fire along the coast in the Santa Monica Mountains than in the inland valleys of the Riverside–Perris Plain. Near Ramona in San Diego County, Bradbury (1974) found that CSS invaded chaparral in areas of chronic disturbance but found little change in CSS cover and species composition. In a vegetation-mapping survey from aerial photographs in 1928–36 and 1980, Freudenberger et al. (1987) found that grassland had increased in some

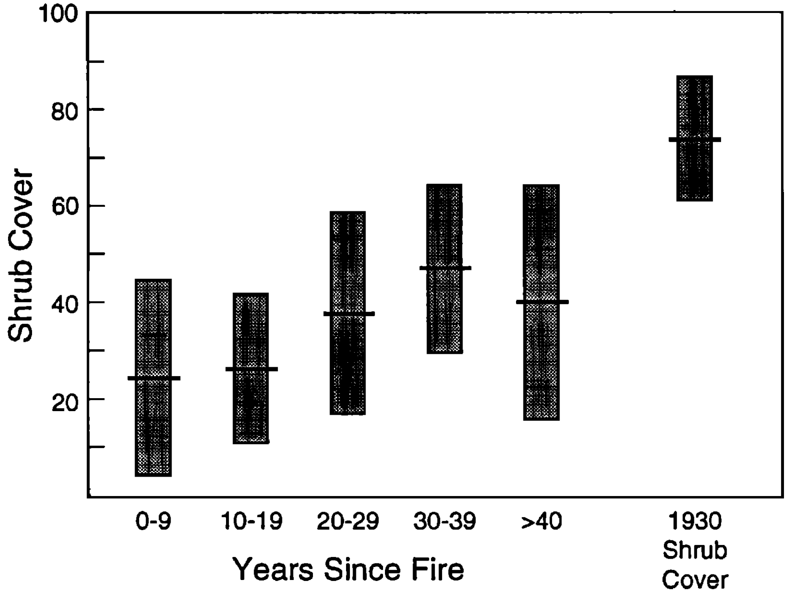

Figure 6. Chronosequence of postfire shrub cover.

places of the Los Angeles Basin but that CSS replaced grassland in others. Seedling densities were high in CSS stands but low outside their boundaries.

CSS appears to be susceptible to profound change, even over short time scales, because of its extensive coexistence with invasive exotic annual grasses. Invasions of exotic annuals into CSS have been attributed to anthropogenic disturbance (Gulmon 1977, Freudenberger et al. 1987, Heady 1988, O'Leary and Westman 1988, O'Leary 1990). Since invasions are assumed to be closely associated with disturbance, it is argued that the degradation of CSS depends on excessive burning and overgrazing, which open up stands to penetration by exotics. CSS is able to resist biological invasions because the herbaceous vegetation (including exotics), which proliferates after a fire, is assumed to decline with the maturation of the shrub layer. Alternatively, the invasion by exotics into CSS may also be due to competitive replacement through processes such as competition for moisture and nutrients. Exotics may also shorten fire intervals by increasing the habitat's flammability (Drake and Mooney 1986, Huenneke and Mooney 1989, D'Antonio and Vitousek 1992).

Whether coastal sage scrub is degraded by disturbance or by exotic invasions requires the examination of three factors: (1) the successional dynamics of exotic herbaceous cover, (2) whether the invasion of exotics requires fire disturbance, grazing, or air pollution, and (3) whether anthropogenic ignition rates influence intervals of fire recurrence. Explanations of habitat change must also consider the history of invasion of exotics that compete directly with CSS.

Table 3 Change in Average Shrub Cover in the Riverside–Perris Plain Compared with Time Since Plot Last Burned

		Cover by species (%)					
Change in total shrub cover (%)	Year	*Artemisia californica*	*Encelia farinosa*	*Eriogonum fasciculatum*	*Salvia apiana*	*Salvia mellifera*	*n*
0–10	1932	25.4 (23.7)[a]	5.8 (14.7)	22.8 (15.5)	7.8 (12.0)	11.7 (18.1)	16
	1992	4.6 (7.2)	5.4 (10.0)	4.4 (6.4)	0.6 (1.5)	3.6 (8.1)	
10–20	1932	15.4 (16.4)	9.7 (13.3)	22.0 (17.0)	6.5 (9.5)	14.6 (23.4)	23
	1992	3.3 (3.7)	9.5 (11.3)	9.2 (11.3)	0.7 (1.7)	2.3 (6.6)	
21–40	1932	23.1 (26.2)	1.4 (4.2)	14.5 (10.5)	18.4 (13.2)	2.6 (7.8)	10
	1992	10.0 (8.8)	5.7 (11.3)	14.5 (11.3)	4.2 (8.5)	2.1 (4.9)	
>40	1932	17.1 (16.4)	2.3 (4.9)	22.1 (14.5)	5.1 (9.4)	17.7 (23.8)	29
	1992	8.8 (8.8)	2.1 (4.4)	10.5 (10.3)	3.7 (9.5)	10.4 (18.4)	

[a] Standard deviations in parentheses.

Land Clearing

The assertion that as much as 90% of CSS has been removed for urbanization and agriculture has been based on the assumption that fertile soils of the Los Angeles basin were largely covered by woody vegetation (Westman 1981, Freudenberger et al. 1987). Grasslands were presumed to be focused near Indian settlements and that frequent burning was required to maintain them (Timbrook et al. 1982). The record of indigenous vegetation in the coastal and interior valleys of California, however, is virtually nonexistent because exotic annuals introduced with Spanish colonization in 1769 were displacing native herbaceous cover before scientists first visited the region (Heady 1988). Accounts from the Portolá and Anza expeditions of 1769–1772 suggest that the Los Angeles Basin was covered by extensive herbaceous vegetation (Bolton 1927, 1930, Minnich 1988). In 1796 Juan Crespi and Junípero Serra described large areas of "pasture" in the plains of San Diego (Minnich and Franco-Vizcaíno 1998). Hence estimates of CSS losses may be greatly exaggerated.

History of Invasions of Exotic Plants in California

An important question necessary to evaluating the role of disturbance versus competitive displacement is why the decline of CSS has occurred only during recent decades. Although European exotics have been present in California since Franciscan mission times in 1769, invasive species have

Table 4 Frequency and Average Cover of Shrubs Extirpated from and Immigrating to Vegetation Plots in the Riverside–Perris Plain

Species	*Artemisia californica*	*Encelia farinosa*	*Eriogonum fasciculatum*	*Salvia apiana*	*Salvia mellifera*
No. of plots with species in 1932	66	26	67	38	32
No. of plots where extirpated in 1992	5	2	15	16	8
Percentage of plots where extirpated in 1992	7.6	7.7	22.3	42.1	18.8
Average cover (%) in 1932 in plots where extirpated	42.6 (25.6)[a]	5.0 (5.7)	14.9 (10.8)	12.8 (12.3)	25.2 (23.2)
No. of plots where immigrated	11	11	8	3	3
Percentage of plots where immigrated in 1992	16.7	42.3	11.9	7.9	9.4
Average cover (%) in 1992 in plots where immigrated	4.9 (4.3)	5.0 (5.5)	4.3 (4.1)	2.3 —	7.3 —

[a] Standard deviations in parentheses.

come in "waves" over the past two centuries (Heady 1988), and the ecological requirements of early arrivals were different from later ones, with divergent impacts on CSS.

The first exotics to spread extensively in southern California, notably, *Avena fatua*, *Brassica nigra*, and *Erodium cicutarium*, were introduced by Franciscan missionaries in 1769 or perhaps earlier as ballast from ships. These annuals quickly replaced indigenous herbaceous cover throughout California (Table 5; Heady 1988). For example, the U.S./Mexican boundary survey reports and the Pacific Railroad Surveys in the 1850s found that *Avena fatua*, *Brassica geniculata*, *Erodium cicutarium*, and *Trifolium* spp. were extensively naturalized in coastal southern California, including the San Bernardino Valley (Parry 1859, Minnich 1988). These surveys indicate, however, that exotic annuals were concentrated in bottomland habitats and disturbed places, as seen today, far from the CSS covering the foothills. Indigenous herbaceous vegetation was assumed to be perennial bunch grassland of *Nassella* spp., but historical descriptions, as well as phytolith and archaeological evidence, indicate that some herbaceous cover in southern California and neighboring northern Baja California may have consisted predominantly of forb fields (Bartolome et al. 1986, Bean and Lawton 1973, Timbrook et al. 1982, Minnich and Franco-Vizcaíno 1998).

The second wave of exotic annuals, including mostly *Bromus* spp. and *Brassica* spp., did not reach the Riverside–Perris Plain until the early 20th century. In the San Bernardino Valley, the first records of *Bromus madritensis*, *B. diandrus*, and *Brassica geniculata* date to ca. 1890, when they were found mostly along roadsides and in waste places. These annuals gradually

Table 5 Approximate Arrival Dates of Exotic Annuals in California[a]

Species	Year	Native range
Erodium cicutarium	1600s?	Mediterranean Europe
Avena fatua	1769	Mediterranean Europe
Brassica nigra	1769	Mediterranean Europe
Bromus mollis	1860	Mediterranean Europe
Bromus madritensis ssp. *rubens*	1880	Mediterranean Europe
Bromus diandrus	1880	Mediterranean Europe
Bromus tectorum	1880	Mediterranean Europe
Avena barbata	1880	Mediterranean Europe
Brassica geniculata	1880	Mediterranean Europe
Brassica tournefortii	1927	Northern Sahara Desert
Schismus barbatus	1950	Middle East

[a]After Heady (1988), Parish (1913, 1920).

expanded across valley lowlands only by 1920 (Parish 1913, 1920). In contrast with the first wave of exotics, they spread onto CSS-covered hillsides. They were later joined by still other taxa capable of invading CSS, including *Schismus barbatus* in the 1950s and *Brassica tournefortii* in the 1980s. The evaluation of dynamics in relation to fire, grazing, and air pollution must consider the history of proliferation of exotics.

Fire

Studies in California have shown that CSS is resilient under periodic fire, though most of its plants resprout poorly after being burned. Seedlings must establish themselves from a prefire seed cache (*Salvia apiana*, *S. mellifera*) or germinate from seed dispersed widely by wind (*Artemisia californica*, *Encelia farinosa*, *Eriogonum fasciculatum*). Resprouting species flower vigorously the first few years after a fire, providing nonrefractory seeds that germinate in subsequent years, leading to mixed-aged stands (Westman 1981). Recruitment and growth to maturity is extremely rapid (ca. 10–20 years) for most taxa (Westman 1982).

Disturbance-dependent models state that although early succession is characterized by abundant herb cover, the probability of recurring fire capable of breaching succession and inducing permanent vegetation change is averted by the limited persistence of indigenous herbs. Many herbs are specialized fire annuals that sprout from a dormant seed pool whose germination is stimulated by the heat of fire, charred wood, and light (Westman 1979, Keeley and Keeley 1984, O'Leary and Westman 1988). The decline of the herb layer improves the chances for the long intervals between fires compatible with the life-history traits of CSS species. However, there is uncertainty whether natives are fire annuals *sensu stricto*. Accounts by C. R. Orcutt and others of extensive flower fields before the second invasion of exotics (Minnich and Franco-Vizcaíno 1998) suggest that wildflowers may be more generalized, or germinate to cues of precipitation and temperature, like closely related desert wildflowers, as well as from fires.

Table 6 Total and Native Biomass and Shrub Cover by Time Since Fire in the Box Springs Mountains, Riverside[a]

			Biomass (tons/ha)		
Site and year	Precipitation (cm)	Years since fire	Total	Native	Shrub cover (%)
Two Trees Canyon					
Site 1					
1989	16.4	1	1.59	0.81	1.1
1990	14.0	2	0.62	0.51	–[b]
1991	26.3	3	2.56	2.13	–
1992	28.1	4	1.80	1.15	–
1993	52.8	5	3.31	1.34	12.4
1994	23.7	1	2.49	0.52	0
1995	48.0	2	2.92	0.41	0
Site 2					
1989	16.4	8	2.32	1.45	29.3
1990	14.0	9	0.57	0.02	–
1991	26.3	10	3.39	0.08	–
1992	28.1	11	2.31	0.08	–
1993	52.8	12	2.53	0.07	12.4
1994	23.7	1	2.41	0.04	0
1995	48.0	2	2.31	0.09	0
Box Springs					
Site 1					
1990	14.0	1	1.06	0.18	0
1991	26.3	2	2.22	0.41	–
1992	28.1	3	2.11	0.08	–
1993	52.8	4	1.64	0.10	5.4
1994	23.7	1	1.45	0	0
1995	48.0	2	2.03	0.06	0
Site 2					
1990	10	0.37	0	29.7	
1991	11	2.90	0.27	–	
1992	12	1.49	0.09	–	
1993	13	0.55	0.03	44.9	
1994	14	0.49	0.01	–	
1995	15	0.95	0.03	44.8	
Mean	25.4				

[a] Data from transects taken annually at the end of spring growth flush between March and early May.

[b] No data.

Many forbs may decompose and their stems may fragment during summer drought because they lack the silica content critical to the curing and flammability of grasses (D'Antonio and Vitousek 1992).

Field sampling for herb cover in the Box Springs Mountains, near Riverside, from 1989 to 1995 (Table 6) shows that annuals form high biomass within the first growing season after fire, reducing bare zones for shrub establishment. Native annuals (mostly *Phacelia distans*, *Cryptantha intermedia*, and *Emmenanthe penduliflora*) proliferated after a spring burn at one site but were replaced within 5 years by a dense cover of exotic annuals (*Bromus madritensis*, *Avena barbata*, *Erodium cicutarium*, *Schismus barbatus*, *Brassica geniculata*, and *B. tournefortii*), further preventing the development of the bare zones necessary for shrub establishment. Succession after a summer burn in Box Springs Canyon was dominated by exotic annuals from the start. *Erodium cicutarium* and *Schismus barbatus* were dominant the first two years, *Bromus madritensis* and *Avena barbata* thereafter. The persistence of herbaceous biomass was associated with shrub cover of 5 to 12% after 4 or 5 years. Shrub cover decreased from 29 to 12% after 10 years at one site from the combined effects of drought and freeze mortality. At yet another site, exotic annuals produced 1.5–3.0 tons/ha for 12 years after fire until the shrub layer reached canopy closure (shrub cover increased from 27 to 44% between 1990 and 1995).

Some studies indicate that fire at intervals <5–10 years will likely eliminate sage scrub, leading to domination by nonnative grasses (Wells 1962, Kirkpatrick and Hutchinson 1980, Keeley 1981, Zedler et al. 1983, Malanson 1984, Freudenberger et al. 1987, O'Leary and Westman 1988), although others have come to the opposite conclusion (Griffin 1978, Davis et al. 1988, Callaway and Davis 1993). It has been argued that the invasion of exotics has been prompted by anthropogenic burning because the rarity of lightning at low elevations makes natural fire too rare (Keeley 1981). Prehistoric fire intervals in CSS are unknown. However, electromagnetically recorded lightning-detection rates in the region are 0.5 to 1.0 strikes per kilohectare per year, and a 2–4% success rate in the initiating fires (suppressed lightning fires/lightning detections), typical of the nearby mountains, yields a fire-establishment rate requiring suppression of 1 per kilohectare every 30 years (Minnich et al. 1993). Fires in grassland can be much larger than in sage scrub because grasslands constitute a fire hazard at the landscape scale regardless of their history. Hence relatively few ignitions can lead to extensive burning. In the Box Springs Mountains, exotic annuals supported fires in 1989, 1993, and 1995, with the biomass levels of ±1.5 tons/ha. Since this level of biomass was reached with annual precipitation as low as 16.4 cm, 65% percent of normal (Table 6), herbaceous fuel build-up may be sufficient to carry fire most years. Three sampling sites had burned two to four years within the seven-year sampling period. Similarly, frequent fires in San Diego County were encouraged by deliberate seeding of the inflammable exotic grass *Lolium multiflorum* (Zedler et al. 1983).

In the Riverside–Perris Plain, California Division of Forestry records (on file at Perris) and Landsat imagery (Minnich 1983) show that fires carried primarily by exotic annual grassland have been frequent and extensive over the past 40 years, with the majority of VTM plots having burned during the past 20 years. VTM replicate chronosequences show that all CSS dominants are capable of reestablishing themselves soon after a fire. Only *Encelia farinosa*, however, has achieved the cover values reported in the original survey, and often within 10 years after fire. Other shrubs had not reached VTM levels by 40 years.

The divergence in succession patterns by slope is seen on Box Springs Mountain (Table 7). South-facing slopes experience rapid establishment of virtually monotypic stands of *Encelia farinosa*, with shrub cover increasing to 60% and shrub density to 9687 per hectare by 14 years after a fire. Although we observed low rates of resprouting in *Encelia farinosa* (±10%), as many as 11,000 seedlings/ha established themselves within a few years, apparently through long-range wind dispersal of seeds. Seedling establishment diminished with increasing shrub cover, especially after 5 years. The resilience of *E. farinosa* may be related both to its resprouting ability and to its preference for xeric southern exposures where herbaceous cover is limited. On north-facing slopes, CSS cover was ±2.2% and densities were ±500 stems/ha, even in stands as old as 12 years. *Eriogonum fasciculatum*, *Artemisia californica*, and *Salvia apiana*, which were mapped as dominants on these sites by the VTM survey, apparently were burned almost totally, and the establishment of seedlings of these species that must regrow from seeds is apparently limited by the dense cover of *Bromus diandrus*. Moreover, there is little evidence that canopy closure reduces herb cover. Hence another grass fire is a virtual certainty before the development of a shrub canopy. Postfire succession may also be further postponed by increasing lag times due to the need for long-range seed dispersal from increasingly scarce surviving populations.

These trends are similar to postfire successions in inland Riversidian sage scrub recorded in other studies (Kirkpatrick and Hutchinson 1980, O'Leary

Table 7 Sequence of Postfire Succession of Coastal Sage Scrub in the Box Springs Mountains

Site	Years since fire	Cover (%)[b]			Stem density[c]				Seedling density[d]			
		En	Ef	Total	En	Ef	Ac	Total	En	Ef	Ac	Total
South-facing slopes[e]												
Sug94S	1	24.2	0	24.2	2760	0	0	1760	11,000	0	0	11,000
TT93S	2	4.8	0	4.8	900	0	0	900	3000	0	0	3000
Sug88S	7	35.6	0	35.6	2297	100	0	2397	1000	0	0	1100
Sug83S	12	42.4	0	42.4	4386	0	0	4386	0	0	0	0
Belv81S	14	35.4	0	35.4	2300	0	0	2300	1100	0	0	1100
Sug81S	14	66.2	1.6	67.8	9203	242	242	9687	0	0	0	0
North-facing slopes												
TT93N	2	0	0	0	20	20	200	240	0	0	100	100
Sug88N	7	0	0	0	0	0	0	0	0	0	0	0
Sug83N	12	0	2.2	2.2	0	500	0	500	2220	100	0	100
Sug81N	14	0	0	0	0	0	0	0	0	0	0	0
Belv81N	14	0	0	0	160	20	20	200	0	0	0	0

[a] En, *Encelia farinosa*; Ef, *Eriogonum fasciculatum*; Ac, *Artemisia californica*.

[b] Based on 50-m line-intercept transects.

[c] Expressed as stems per hectare and based on 50-m point-center quarter transects.

[d] Expressed and seedlings per hectare and based on 1.8-m circle plots on 10 points of point-center quarter transects. Seedlings were <10 cm tall with no charred stems at the root axis that would indicate resprouting.

[e] Slope aspect divided hemispherically with northern exposures (clockwise) from 270° to 90° and southern exposures from 90° to 270°.

and Westman 1988) and contrast with the resilience of sage scrub near the coast (Malanson and O'Leary 1982, 1985, Malanson 1984, O'Leary and Westman 1988). Along the coast, sage scrub shrubs, even some of the same or closely related species (*Artemisia californica*, *Salvia leucophylla*, *Eriogonum fasciculatum*, and *Encelia californica*) resprout better. Seedling establishment began in the second growing season after fire from the fruiting of shrubs resprouting the first year.

Grazing

Thinning of CSS has been attributed to livestock grazing, which opens up the shrub canopy to invasion by exotic annuals, disseminates seeds, and reduces the ability of native forbs and perennial bunch grasses to compete with exotics (McBride 1974, Freudenberger et al. 1987, O'Leary and Westman 1988). Historically, grazing was heaviest during the late 19th century. Livestock grazing in the Riverside–Perris Plain consisted of winter sheep drives beginning in the 1860s, reaching a peak near 1900 (Minnich 1988). Evidence is seen in criss-crossing trails ("sheeptours") on hillsides. However, grazing declined by the early 20th century—before the widespread naturalization of "second wave" exotics, including *Bromus* spp., and before the decline in CSS—because the annual transhumance grazing cycle was interrupted by the prohibition of summer browsing in the mountains with the establishment of national forests of southern California (Lockmann 1981). During our resurvey only two plots were subject to intense sheep grazing (Arlington Mountain, Massacre Canyon). Exotic grasses at these sites were browsed to the ground, and shrub seedlings appear to be eliminated by domestic stock, recalling of the impacts of grazing by feral goats and sheep on the Channel Islands (Brumbaugh 1980, Minnich 1980, Van Vuren and Coblentz 1987). Alternatively, the proliferation of exotics in southern California's inland valleys suggests that these plants were able to occupy suitable undisturbed habitat. For example, there is evidence that "first wave" invasions preceded settlement in the Central Valley (Wester 1975, 1981). Livestock disturbance and agricultural clearing have only a short-term role in the spread of these weeds (Biswell 1956, Naveh 1967, Heady 1988, Sauer 1988, Huenneke and Mooney 1989, Huenneke et al. 1990, D'Antonio and Vitousek 1992).

Competitive Exclusion

Aerial photographs and VTM-quadrat replications reveal shrub losses in stands last burned >40 years ago. Hence, while fire and grazing may facilitate conversion of CSS to grass, the deterioration of CSS may be more fundamentally related to competitive exclusion, in which exotics themselves induce habitat changes. Means for this include resource competition, light absorption, water uptake, altered water-holding capacity, and nutrient uptake (D'Antonio and Vitousek 1992). Exotic grasslands may be inducing nutrient and moisture regimes that inhibit the establishment, growth, and persistence of native shrubs (Westman 1981, O'Leary and Westman 1988). In the Riverside–Perris Plain, three lines of evidence support the view that exotics outcompete CSS.

(1) High shrub mortality during the 1992 replicate survey. In 22 plots (28% of VTM plots) the cover of dead shrubs was greater than 10%. Mortality followed drought between 1984 and 1990, during which time the water demand of dense, shallow-rooted exotics may have limited the water reaching the shrubs' roots. Shrub mortality may be related to the ability of herbs to produce high biomass (high water demand) in winters with subnormal precipitation. Although herb biomass was <0.6 tons/ha in the drought year of 1990, annual productivity was 2.5 tons/ha in the dry years of 1989 and 1994 (Table 6) owing to well-distributed light rains. Mortality in old-growth stands may be related to the large canopy and leaf area (transpiration load) of the shrub layer. We observed little shrub mortality in plots with low annual cover, mostly on rocky outcrops and on gabbro basalts. Soils overlying gabbro basalts may contain toxic chemicals or be deficient in nutrients, adversely affecting both exotic and native annuals, like soils lacking vital nutrients at Jasper Ridge in central California (Huenneke et al. 1990).

(2) CSS/grassland ecotones follow slope lines independent of fire history. These trends indicate a pattern of variable recruitment rates with habitat change unrelated to disturbance (unpublished data).

(3) Dense, relatively diverse stands of CSS (*Artemisia californica*, *Eriogonum fasciculatum*, *Encelia farinosa*) often grow on recent road cuts and are often immediately surrounded by dense grasslands on undisturbed soils. Apparently, the scraping of topsoils and exposure of coarser decomposed regolith with nutrient characteristics of the basement encourages the rapid invasion of coastal sage species. Colonization of road cuts by CSS, far removed from neighboring stands, also suggests that long-range seed dispersal is not limiting even with low resprouting rates (O'Leary and Westman 1988) because these shrubs have tiny seeds capable of wind dispersal. Perhaps the absence of *Salvia mellifera* and *S. apiana* in road cuts reflects their seeds' larger size (Hickman 1993) and limited dispersal abilities. Except at sites occupied by *Encelia farinosa*, patterns of CSS reestablishment after fire on the Riverside–Perris Plain are inconsistent with the view that weedy invaders are eliminated rapidly by shading from larger, longer-lived native species (Huston 1995).

Air Pollution

Two major air pollutants, ozone and nitrogen oxides, may affect CSS (Westman 1979, 1981, Allen et al. 1996, Padgett et al. in press). Figure 7 shows a north-to-south gradient in the CSS losses in the Riverside–Perris Plain. For example, most VTM plots near Riverside have <20% of former cover, whereas cover was nearly stable at several plots to the south. The concentration of air pollution in the region varies widely (Allen et al. 1996, Padgett et al. in press). During summer, thermal gradients produced by the combination of daytime heating of the land and cool air overlying the ocean draw the marine layer into the inland valleys, with vertical mixing limited by strong temperature inversions. Blockage of onshore marine air flow by the Santa Ana Mountains divides the air mass into more and less polluted halves, with polluted marine air moving into the north from the urbanized Los Angeles Basin and less polluted air entering the south from less populated

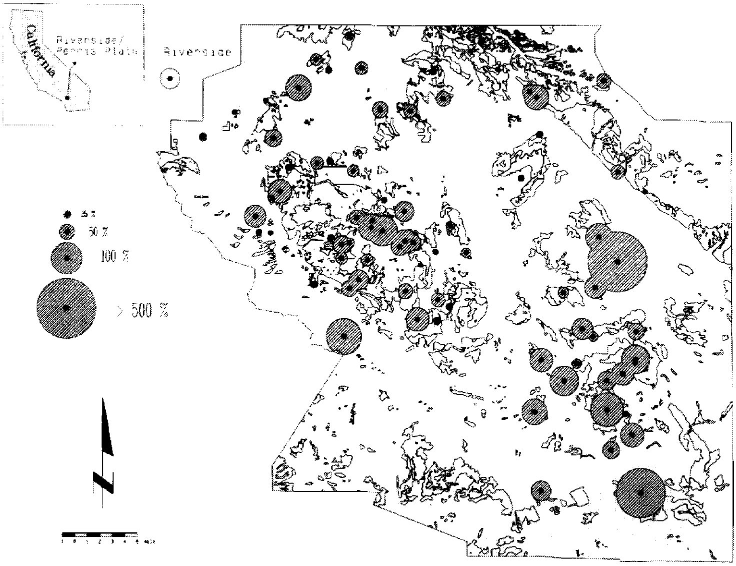

Figure 7. Change in the cover of coastal sage scrub on VTM plots from 1932 to 1992.

coastal regions. The two air streams frequently converge near Perris, 15 km southeast of Riverside, yielding a discontinuity in air-pollution concentrations and visibility.

How specific air pollutants may influence CSS is unclear. In the greenhouse, Preston (1986) and Westman et al. (1986) found simulated ambient summer ozone concentrations to reduce the growth of well-watered CSS seedlings. They concluded that air pollution weakens the shrubs, lowering their resprouting ability. However, there is no baseline data on the sprouting ability of CSS in the Riverside–Perris Plain before air pollution. Alternatively, differences between coastal and inland sites in resprouting rates may reflect local genetic variability, as well as climatic differences, including higher humidity, lower rates of leaf fall, and more green foliage during the summer drought along the coast. Postfire successional response may also be related to climatic gradients. CSS resilience along coast may be related to higher shrub productivity sustained by warmer temperatures through the winter rainy season. Growth persists into late spring because of the cooler summer. In the Riverside–Perris Plain, cold winters limit productivity until March/April when warming temperatures combined with moist soils result in a brief flush of growth. Growth is terminated by high temperatures beginning usually in May. Air-pollution effects may also be limited because summer ozone concentrations do not reach high levels until after shrubs have experienced desiccation, stomatal closure, and leaf senescence (Allen et al. 1996, Padgett et al. in press).

Anthropogenic nitrogen deposition may alter the composition of soil microorganisms and encourage displacement of native forbs by nitrogen-demanding exotics. In the Central Valley of California, the invasion of exotics was encouraged by high nutrient availability, independent of physical disturbance (Huenneke et al. 1990). Hence, increased soil nitrogen may make CSS more susceptible to invasion by exotic plants. CSS may decline because of elevated nitrate plus ammonium levels in the soil and the air (Allen et al. 1996, Padgett et al. in press). Studies have yet to control for air pollution by examining the effects of exotics growing in areas of low pollution, such as the California deserts and coastal northern Baja California.

Alternatively, differences in CSS losses in the Riverside–Perris Plain may be related to substrate. Gabbro basalt, the substrate on which CSS is most stable, occurs over large areas in the southern basin but is virtually absent in the north. Granitic substrate is widespread in polluted areas north of Perris. Exotic annuals have also spread extensively into the CSS of northern Baja California, where air pollution is virtually absent (Minnich and Franco-Vizcaíno 1998). Future research on the effects of air pollution should control for the role of substrate and changes in soil chemistry.

MANAGEMENT IMPLICATIONS

A fundamental question in the management of CSS is whether the present decline is due to anthropogenic disturbance or to competitive displacement by exotic annuals. Limited chronosequence sampling of shrub and herb cover in the Box Springs Mountains supports both models, depending on the site. *Encelia farinosa* recovers rapidly, with corresponding decreases in herbaceous cover, even with short intervals between fires, but this shrub is only locally abundant in the northern Riverside–Perris Plain. In contrast, stands dominated by *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia mellifera,* and *S. apiana* recover poorly even with little disturbance. The widespread decline of CSS in the Riverside–Perris Plain independent of disturbance supports the competitive-displacement hypothesis. The future of the Riverside–Perris Plain may see the displacement of CSS by exotic annuals.

To protect species diversity, the Riverside County Habitat-Conservation Plan for the Riverside–Perris Plain has purchased primarily lands contiguous with preexisting public lands, including lakes Matthews, Perris, and Skinner (Feldman 1995). These measures may not serve to protect the California Gnatcatcher. The assumption in preserve design and land management of static CSS distributions, stand structure, and species diversity is refuted by our replication of the VTM. Therefore, critical examination this dynamic one-way process of CSS conversion to exotic annual grassland is needed in preserve selection. Otherwise, land-protection measures will result in grassland preserves with little CSS flora or fauna. Most CSS on public land is now experiencing stand-thinning and potential displacement by exotic annual grassland. The plain's largest remaining dense CSS, on gabbro basalts, are less susceptible to grass invasion and have stable shrub communities but are in private ownership and endangered by urban development.

SUMMARY

Californian coastal sage scrub (CSS) has been extensively cleared for agriculture and urbanization. Few studies have examined the landscape-scale dynamics of surviving CSS, particularly in relation to invasive exotic annuals. From 1929 to 1934 the vegetation of California was inventoried by the Vegetation Type Map (VTM) Survey. We replicated the VTM to quantify the changes in the CSS in the Riverside–Perris Plain over the past 60 years. The cover of *Encelia farinosa* cover was stable, but that of *Salvia apiana*, *S. mellifera*, and *Artemisia californica* was reduced greatly. At many sites, former dense shrub cover had become open stands with a continuous layer of exotic annuals dominated by either *Bromus diandrus* or *B. madritensis* ssp. *rubens*. *Encelia farinosa* reestablished itself rapidly on south-facing slopes, but on north-facing slopes the dense cover of the exotic grass *Bromus diandrus* limited reestablishment of *Eriogonum fasciculatum* and *Artemisia californica*. CSS has declined under limited or no grazing pressure from livestock. Hence, while fire and grazing may facilitate CSS-to-grass conversion, in some cases the deterioration of CSS may be more fundamentally related to competitive exclusion. Exotics may alter nutrient and moisture regimes, inhibiting the establishment, growth, and survival of native shrubs. Our data refute the assumption that CSS is still a stable habitat in this area. Attempts to conserve the California Gnatcatcher by extending public lands in regions experiencing this type of habitat degradation may be insufficient and need to be reexamined.

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