SEVEN

Northern Coastal Scrub and Coastal Prairie

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Introduction

Northern coastal scrub and coastal prairie exist in a continuum of herbaceous to dense woody shrub cover wherever the cooling influence of the Pacific Ocean moderates summer drought (Fig. 7.1) from Northern Santa Barbara County north to the Oregon border and inland to the Sierra Foothills. Once widespread, now these habitat types are increasingly rare and endangered. Ironically, in many cases it is the coastal scrub that endangers the rare coastal prairies, as shrubs invade grasslands in the absence of grazing and fire. Because of the rarity of these habitats, we are seeing increasing recognition and regulation of them and of the numerous sensitive species reliant on their resources.

In this chapter, we describe historic and current views on habitat classification and ecological dynamics of these ecosystems. As California's vegetation ecologists shift to a more quantitative system of nomenclature, we suggest how the many different associations of dominant species that make up each of these systems relate to older classifications. We also propose a geographical distribution of northern coastal scrub and coastal prairie, and present information about their paleohistoric origins and landscapes. A central concern for describing and understanding these ecosystems is to inform better stewardship and conservation. And so, we offer some conclusions about the current priorities for conservation, information about restoration, and suggestions for future research.

Northern Coastal Scrub

Classification and Locations

Among the many California shrub vegetation types, "coastal scrub" is appreciated for its delightful fragrances and intricate blooms that characterize the coastal experience. It is sometimes referred to as soft chaparral because of its flexible stems and foliage, herbaceous understory, intergradation with coastal prairie, and smoother appearance in the landscape (Jepson 1925). This contrasts to the stiff, leathery, and rough characteristics of the "hard" chaparral types (Holland and Keil 1995, 161; Ornduff, Faber, and Keeler-Wolf 2003, 164). Ecologists generally recognize northern and southern divisions of coastal scrub corresponding mainly to the shift from cooler-moister to warmer-drier climates, and in species composition (Holland and Keil 1995:155). The northern division generally corresponds to

FIGURE 7.1 Mosaic of northern coastal scrub and coastal prairie at the Landels-Hill Big Creek Reserve along the Big Sur coast. Photo courtesy of L.D. Ford.

the Franciscan, Lucian, and Diablan divisions of Axelrod's (1978, 1118) "northern coastal sage," which transitions to the Venturan division within the "southern coastal sage." In Central California the northern and southern types commonly occur adjacent to each other at edaphic and microclimatic ecotones in the Central Coast Ranges.

Munz and Keck (1959, 13) popularized the term "northern coastal scrub." They described dense stands of shrubs and forbs, often mixed with extensive areas of coastal prairie, situated between coastal strand and redwood forest along the California coast north of Big Sur. Northern coastal scrub occurs farther south and more broadly than Munz and Keck acknowledged—in discontinuous bands along the coastal terraces and the low to middle slopes of the outer Coast Ranges, from Northern Santa Barbara County north to Southern Oregon, including the coastal islands from the Northern Santa Barbara Channel north to the San Francisco Bay (Fig. 7.2). Within these same latitudes inland from the coast, it occurs on the lower slopes and valley bottoms of the middle and inner Coast Ranges. It also extends inland (with less diversity) from the Golden Gate through the Coast Ranges on the hillside margins of Suisun Bay and the Sacramento-San Joaquin Delta and up the Sierra Nevada Foothills to more than 300 m elevation. It has been observed in scattered stands in the foothills of Placer, El Dorado, Amador, and Calaveras counties. This distribution follows the "blankets" and "corridors" of marine climate influence (zones of coastal fog or cool moist marine air) that press inland from the coast with the prevailing winds.

FIGURE 7.2 Generalized map of northern coastal scrub and coastal prairie in California. Sources: Outline map from Information Center for the Environment, University of California, Davis (1997); vegetation distribution after Ornduff, Faber, and Keeler-Wolf (2003), Axelrod (1978), and personal observations of the authors.

Potential distributions of northern coastal scrub and coastal prairie roughly correspond in relation to this climate zone.

Northern coastal scrub usually occurs at <500 m elevation in the coolest and most mesic habitats of any of the coastal scrub types (Holland and Keil 1995, 157). Soils vary widely, including well-weathered clay and shallow coarse soils and stabilized sand dunes. The soils are typically higher in salt concentrations than in surrounding areas due to exposure to the marine air. Coyote brush *(Baccharis pilularis)*, the characteristic species of northern coastal scrub, accumulates high concentrations of salts in foliage and roots from exposure to aerosol fallout, which in turn adds continually to the salt concentration of the soils (Clayton 1972). Northern coastal scrub commonly occurs on thicker soils and moister aspects than southern coastal scrub or chaparral in the Central Coast Ranges, and where it occurs adjacent to the other two types, northern coastal scrub is usually at a lower elevation. The southern coastal scrub elements are typically more drought deciduous than the northern elements (Axelrod 1978, 1119). On sites of thicker soil and more moisture, northern coastal scrub is commonly found in a matrix with open meadows or patches of coastal prairie or annual grassland. It commonly invades and replaces these grasslands, the result of natural succession after the cessation of frequent fire and livestock grazing. Coyote brush is typically the first colonizer and remains the sole community member of such stands until other member species establish (Howell 1970, 14).

We include at least 9 distinct series (alliances) and 30 related associations recently identified by the California Department of Fish and Game (CDFG 2003) as subdivisions of northern coastal scrub (Table 7.1). These large numbers correspond to the diversity of microclimates, soils, landscape positions, paleohistory, disturbance history, land-use history, and adjacent vegetation types of the region. We defined this collection of principal series and associations from among many more based on representation of the most important woody species, predominant distributions at lower to middle elevations on the north and central coasts within the "coastal scrub" zones, and relationships in ecological succession.

The geographic relationships of the combined set of recognized and potential subdivisions of northern coastal scrub may be appreciated best in a generalized map representing proximity to the coast and marine influences, topographic position, and relative position (Fig. 7.3).

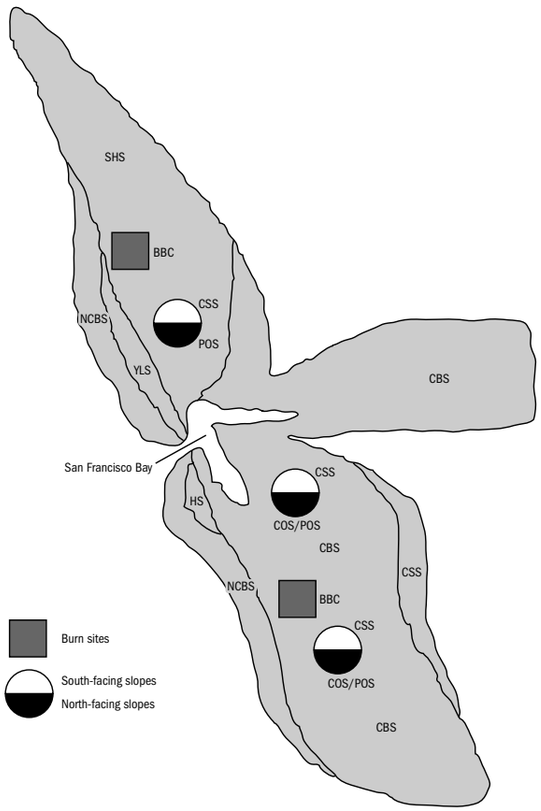

FIGURE 7.3 Conceptual map of relative landscape positions of the northern scrub series in northern and central California. Series acronyms: BBC = blue blossom chaparral; CBS = coyote brush scrub and dwarf scrub; COS = coffeeberry scrub; CSS = California sagebrush scrub; HS = hazel scrub; NCBS = northern coastal bluff scrub; POS = poison oak scrub; and YLS = yellow bush lupine scrub.

NORTHERN COASTAL BLUFF SCRUB

On coastal bluffs and rocky headlands in a discontinuous and very narrow band, northern coastal scrub intergrades to distinct stands with shorter stature, more succulent foliage, and an additional set of salt-tolerant species ("northern coastal bluff scrub" of Cheatham and Haller 1975; and "sea-bluff coastal scrub" of Holland and Keil 1995, 167). Most of the woody species are evergreen or partially drought-deciduous. The composition and structure of the important succulents, shrubs, and herbaceous plants in this series are unique, although it is not clearly segregated from coyote brush scrub in the classification of Sawyer and Keeler-Wolf (1995, 142). Keeler-Wolf (personal communication) reports that recent observations indicate coastal bluff scrub is often a mixture of adjacent series and represents multiple associations, including those with coyote brush and other common shrubs of northern coastal scrub plus *Eriogonum latifolium*, *Coreopsis gigantea*, *Dudleya caespitosa*, *Erigeron glauca*, and others, but correct classification awaits formal studies. These communities often occur on vertical cliff faces and terraces near the shore where the influences of unstable substrate and marine climate (cool, moist, salt-laden air) are greatest and soils accumulate salts. It is extensive and well developed in the Channel Islands due to the north and east-facing sea cliffs that augment shade and soil moisture (Schoenherr, Feldmeth, and Emerson 1999, 212). It might have been more extensive there prior to settlement due to its sensitivity to livestock grazing.

CALIFORNIA SAGEBRUSH SCRUB

Distinct stands with canopies dominated by California sagebrush *(Artemisia californica)* are commonly found on the margins of coyote brush scrub at the eastern margins of marine influences in the Inner Coast Ranges and on drier slopes in the Central Coast Ranges, particularly near the intergrades of northern to southern coastal scrub (Holland and Keil 1995, 159–161). Nearby stands are often dominated by other common shrubs of northern coastal scrub in addition to a large component of California sagebrush. In such cases, where California sagebrush is less important, the stand may be classified as another series. In the Los Padres National Forest, California sagebrush dominates the canopy of this series with 52% average cover among a wide variety of other less frequent shrubs (Borchert et al. 2004). Despite the affinity of many of these shrubs to southern coastal scrub (including being partially drought-deciduous), we include it as northern coastal scrub because of the importance of California sagebrush in most series of northern coastal scrub.

Soils of these sites are usually shallower than at coyote brush scrub sites. Howell (1970, 12) described California sagebrush as more common on the drier slopes in patches within a landscape dominated by coyote brush. The shallower soil and drier aspect factors appear to facilitate a reduction in coyote brush and favoring of California sagebrush in these margins and patches. Additional research is needed to clarify this effect.

COYOTE BRUSH SCRUB

This series, with the largest number of associations (17), is the most common in the region and best known. It is characterized by coyote brush and a somewhat indistinct assemblage of shrub, sub-shrub, and herbaceous understory associates (Holland and Keil 1995, 157). In Humboldt and Del Norte counties, Belsher (1999) found stands of this series on steep rocky areas of bluffs and terraces. Such sites were most exposed to salt aerosols. Canopies varied from dense and closed with sparse understories to discontinuous with dense herbaceous understories. At Ring Mountain Preserve in Marin County, Fiedler and Leidy (1987) found coyote brush occupied up to 59% cover in a mix with valley grassland, which occupied up to 45% cover. Keeler-Wolf, Schindel, and San (2003) described numerous coyote brush associations at the Point Reyes National Seashore and the Golden Gate National Recreation Area. On the San Mateo County coast, Baxter and Parker (1999) found that coyote brush and seaside woolly-sunflower *(Eriophyllum staechadifolium)* co-dominated the canopy of this series with 67% cover (combined), and small (<1 m^2) canopy gaps occupied more than half the area. Understory species composition and abundance was strongly influenced by the percentage of canopy gap (light penetration).

In the Los Padres National Forest, Borchert et al. (2004) found coyote brush dominated such stands with 71% average cover. They found coyote brush scrub on well-drained Mollisols, Entisols, and Alfisols, including sandy loams and sandy clay loams, and on deeper soils than sites with higher proportions of California sagebrush. On the lower coastal terraces of northern Santa Cruz County, Pollock and Dolman (1991) found coyote brush occurred with an average frequency of 21%, seaside woolly-sunflower 12%, and poison oak *(Toxicodendron diversilobum)* 10%. Important shrubs are shared with neighboring communities, such as seaside woolly-sunflower, an evergreen, with northern coastal bluff scrub. Chaparral shares poison oak, coffeeberry *(Rhamnus californica)*, and yerba santa *(Eriodictyon californicum)*; the first, winter-deciduous; and the latter two, evergreen. Southern coastal scrub shares California sagebrush, deer weed, and sticky monkey flower *(Mimulus aurantiacus)*, all partially drought-deciduous.

In the coastal area south of Big Sur to Northern Santa Barbara County, Holland and Keil (1995, 163) define such stands as southern coastal scrub, but we think the composition clearly makes those coyote brush scrub. The transition there reflects coyote brush's southern limit and the northern limits of several distinct southern coastal scrub shrubs. In the Northern Channel Islands coyote brush is abundant and replaces shrubs more typical of southern coastal scrub to an extent suggesting that area's northern affinity to coyote brush scrub (Schoenherr, Feldmeth, and Emerson 1999, 204).

Coyote brush is inhibited by overstory shading, such as where a tree canopy develops within the scrub stand, and rarely occurs in woodland or forested types (Wright 1928). Some understory species of coyote brush scrub grow under the canopy of coniferous forests (Holland and Keil 1995, 158). Within the same zone as coyote brush scrub, oak woodland commonly occurs with a shrub understory similar to coyote brush scrub, but often without coyote brush itself and with an herb-rich layer (McBride 1974). Coyote brush scrub in the Berkeley Hills is commonly invaded by coast live oak *(Quercus agrifolia)*, which can eventually succeed into oak woodland and replace the scrub (McBride 1974). The shrub and oak mix is recognized as a distinct association of coyote brush scrub, but is part of the grass-brush-woodland succession described below.

A survey by Barbour and Taylor (described in Heady et al. 1977, Table 21-7) suggests a north–south gradient of coyote brush scrub species. An herbaceous and woody understory is well developed in the Northern California range and diminishes south of the Golden Gate. South of the San Francisco Bay, it sometimes lacks the understory and incorporates drought-deciduous southern coastal scrub elements. McBride (1974) found coyote brush scrub of the Berkeley Hills nearly free of an herb layer, except where stands were fairly open or young, such as in the early stages of succession from grassland to shrubs; in those cases, the herb layer was composed of Berkeley Hills grassland species.

At Point Reyes, Grams et al. (1977) found that coyote brush dominated the canopy of this series on north-facing slopes, while both coyote brush and coffeeberry dominated on south-facing slopes. On the south-facing slopes they

TABLE 7.1
Classification, Special-status, and Distribution of the 9 Principal Series (Alliances) and 30 Associations of Northern Coastal Scrub

Floristic Series and Associations	*Corresponding Holland Types*	*Distribution*[a]
(Natural Diversity Data Base: CDFG 2003)	(Holland 1986)	(Sawyer and Keeler-Wolf 1995)
Northern Coastal Bluff Scrub (NCBS) 31.100	Northern Coastal Bluff Scrub	o-NorCo o-CenCo
California Sagebrush Scrub (CSS): 32.010.01 California Sagebrush *[Artemisia californica]* 32.010.02 California Sagebrush-Deer Weed *[Artemisia californica-Lotus scoparius]*	Northern (Franciscan) Coastal Bluff Scrub Central Lucian Coastal Scrub Diablan Sage Scrub	CenCo
Coyote Brush Scrub and Dwarf Scrub (CBS): *32.060.01 Coyote Brush/Seaside Woolly-Sunflower *[Baccharis pilularis/Eriophyllum staechadifolium]*	Northern Dune Scrub Northern (Franciscan) Coastal Bluff Scrub	o-NorCo o-CenCo o-SoCo
*32.060.02 Coyote Brush/Tufted Hairgrass *[Baccharis pilularis/Deschampsia caespitosa]*	Northern Coyotebrush Scrub	
*32.060.03 Coyote Brush/Creeping Ryegrass *[Baccharis pilularis/Leymus triticoides]*	Central Lucian Coastal Scrub	
*32.060.04 Coyote Brush/Sword Fern *[Baccharis pilularis/Polystichum munitum]*	Diablan Sage Scrub	
32.060.05 Coyote Brush-California Sagebrush *[Baccharis pilularis-Artemisia californica]*		
32.060.06 Coyote Brush-Dune Lupine-Yellow Bush Lupine *[Baccharis pilularis-Lupinus chamissonis-Lupinus arboreus*]		
32.060.08 Coyote Brush/California Figwort *[Baccharis pilularis/Scrophularia californica]*		
32.060.09 Coyote Brush/Annual Grasses [*Baccharis pilularis-Bromus* spp.]		
*32.060.10 Coyote Brush/Purple Needlegrass *[Baccharis pilularis/Nassella pulchra]*		
*32.060.11 Coyote Brush/California Oatgrass [*Baccharis pilularis/Danthonia californica]*		
*32.060.12 Coyote Brush/Ocean Spray *[Baccharis pilularis/Holodiscus discolor]*		
*32.060.13 Coyote Brush/Slough Sedge-Common Rush *[Baccharis pilularis/Carex obnupta-Juncus patens]* (Keeler-Wolf *et al.* 2001)		
32.060.14 Coyote Brush-Blueblossom *[Baccharis pilularis-Ceanothus thyrsiflorus]*		
32.060.15 Coyote Brush-California Blackberry/Weedy Herb *[Baccharis pilularis-Rubus ursinus*/Weedy Herb*]*		
32.060.16 Coyote Brush-Coffeeberry *[Baccharis pilularis-Rhamnus californicus]*		

TABLE 7.1 (continued)

Floristic Series and Associations	*Corresponding Holland Types*	*Distribution*[a]
(Natural Diversity Data Base: CDFG 2003)	(Holland 1986)	(Sawyer and Keeler-Wolf 1995)
32.060.17 Coyote Brush-Poison Oak *[Baccharis pilularis-Toxicodendron diversilobum]*		
*32.060.18 Coyote Brush-California Sagebrush-Poison Oak/Coyotemint [*Baccharis pilularis-Artemisia californica-Toxicodendron diversilobum/Monardella villosa]*		
Yellow Bush Lupine Scrub (YLS): 32.080.01 Yellow Bush Lupine-Ripgut Brome *[Lupinus arboreus-Bromus diandrus]* 32.080.02 Yellow Bush Lupine [*Lupinus arboreus*]	Northern Dune Scrub Northern (Franciscan) Coastal Bluff Scrub	o-NorCo
*32.080.03 Yellow Bush Lupine-Heather Goldenbush *[Lupinus arboreus-Ericameria ericoides]*		
32.080.04 Yellow Bush Lupine-Vernal Grass *[Lupinus arboreus-Anthoxanthum odoratum]*		
32.080.05 Yellow Bush Lupine-California Figwort *[Lupinus arboreus-Scrophularia californica]*		
Salal-Black Huckleberry Scrub and Dwarf Scrub (SHS) 32.130 *[Gaultheria shallon-Vaccinium ovatum]*	Northern (Franciscan) Coastal Bluff Scrub Northern Salal Scrub Northern Silk-tassel Scrub Poison-oak Chaparral	o-NorCo OR
Blue Blossom Chaparral (= Scrub; BBC): 37.204.01 Blue Blossom Ceanothus-Coyote Brush-Poison Oak *[Ceanothus thyrsiflorus-Baccharis pilularis-Toxicodendron diversilobum]*	Northern (Franciscan) Coastal Bluff Scrub Blue Brush Chaparral Northern Maritime Chaparral Poison-oak Chaparral	o-NorCo o-CenCo w.l-KlaR OR
Coffeeberry Scrub (COS): 37.920.01 Coffeeberry-Coyote Brush/California Figwort *[Rhamnus californica-Baccharis pilularis/Scrophularia californica]*	Northern Coyotebrush Scrub Central Lucian Coastal Scrub	o-NorCo o-CenCo
Poison Oak Scrub (POS): 37.940.01 Poison Oak-Coyote Brush-Thimbleberry *[Toxicodendron diversilobum-Baccharis pilularis-Rubus parviflorus]*	Northern Coyotebrush Scrub Central Lucian Coastal Scrub	o-NorCo o-CenCo
Hazel Scrub (HS): 37.950.00 Hazelnut *[Corylus cornuta]*	n/a	n/a

NOTE: Asterisks in front of the association name indicate a special status: "rare and worthy of consideration."

[a]Distribution: o-NorCo = outer North Coast; CenCo = Central Coast; o-CenCo = outer Central Coast; o-SoCo = outer South Coast; w.l-KlaR = western low elevation Klamath Ranges; OR = Oregon.

found the understory composition differed from that on the north-facing slopes and had affinities with southern coastal scrub. Keeler-Wolf, Schindel, and San (2003) described coffeeberry dominating scrub stands succeeding from coyote brush dominance. They also found a canopy of Douglas fir *(Pseudotsuga menziesii)* extending over and succeeding coyote brush. Howell (1970, 12) described a diverse "coastal brush" association in Marin County, with different abundances or growth forms of the shrubs according to aspect. He observed poison oak in taller and denser stands on the

moister north-facing slopes and as low bushes on the south-facing slopes. California blackberry *(Rubus ursinus)* was more vigorous on the moister slopes, but also occurred on the drier slopes; California sagebrush and sticky monkey flower were more common on the drier slopes, whereas several sub-shrubs were more common on the moister slopes. We have observed coyote brush scrub of the Big Sur region relatively free of an understory, and coffeeberry more abundant on the north-facing slopes.

OTHER SCRUB TYPES

Yellow Bush Lupine Scrub

The canopies of lupine scrub stands are dominated by either of two *Lupinus* species and usually occur in a grassland matrix restricted to terraces within about 200 m of ocean-facing bluffs. The fast-growing and short-lived yellow bush lupine *(Lupinus arboreus)* can grow tall, but holds a temporary cyclic position across the grassland matrix landscape (Pickart and Sawyer 1998). Shelter from the wind appears to be important in establishment of this species in the windy coastal environment (Gartner 1995). Belsher (1999) found this series in coastal Humboldt and Del Norte counties with equal canopy dominance by coyote brush and yellow bush lupine with understory species less common than in nearby coyote brush scrub. At Bodega Head, Davidson (1975) and Davidson and Barbour (1977) found that the understory was usually absent due to rodent herbivory. Where present, the understory was composed of non-grassland species within canopy openings. The nearly prostrate *Lupinus variicolor* and its associates appeared limited to a narrow bluff-edge zone more exposed to marine influences; it was less successful where it occurred in the yellow bush lupine habitat, which occurred on a second and adjacent narrow band (Drysdale 1971; Pitelka 1974).

Davidson (1975) conducted a demographic study of yellow bush lupine at Bodega Head and concluded that maximum lupine age can be 7 years. Major causes of mortality were drought and mammalian herbivore activity during the first year of growth, and insect herbivore damage later. The insects appear to be episodic in their population densities and can reach such epidemic proportions that entire patches of lupine scrub are killed or denuded in one growing season. Davidson concluded that yellow bush lupine had reached a point of dynamic equilibrium within the grassland and that it was therefore unlikely the grassland as a whole was successional to lupine scrub. Allelopathy did not appear to be a factor in this balance. He attributed the near absence of herbs beneath the lupine canopy to activity by high rodent populations.

Donald Strong and colleagues published a series of papers in the 1990s on their research into the causes of yellow bush lupine crashes. They commented that the intensity of the episodic declines had no known equal with any other plant species anywhere (Strong et al. 1995). Their work extended the list of interacting organisms to include a mini-ecosystem of animals living in soil of the root zone, animals whose activities were invisible above-ground, except for their striking combined effect on bush lupine (Strong 1999; Preisser and Strong 2004).

Salal-Black Huckleberry Scrub and Dwarf Scrub

Like the northern coastal bluff scrub, this series occurs mainly on bluffs, terraces, and slopes on the north coast where marine climate (cool, moist, salt-laden air and wind) influences are strong. Salal *(Gaultheria shallon)* and black huckleberry *(Vaccinium ovatum)* are the most common shrubs. Belsher (1999) found similar vegetation in coastal Humboldt and Del Norte counties, but the canopies were dominated by salmonberry *(Rubus spectabilis)* and thimbleberry *(Rubus parviflorus)*. His "thicket and bramble" occurred in dense stands at forest edges, gullies, and coves where the stands are relatively protected from the stronger winds. Such sites were less exposed to salt aerosols than at coyote brush scrub sites, suggesting these shrubs are intermediate in salt tolerance between coyote brush and conifers. He found that stands with ocean exposure were stable compared to inland stands. On the interregional scale of increasing precipitation and available moisture from central California to Oregon, he found more coyote brush scrub on the coast south of Humboldt County and more "thicket and bramble" on the Oregon coast, with a mix of both on the coast of Humboldt and Del Norte counties.

Blue Blossom Scrub

In stands of this series, blue blossom *(Ceanothus thyrsiflorus)* surpasses coyote brush and other shrubs in proportion of cover and, where stands are dense, it can shade out those shrubs and any understory. It occurs on ridges and upper slopes in scattered stands within a scrub landscape or in the understory of forests (Sawyer and Keeler-Wolf 1995). In Big Sur, Bickford and Rich (1984) and Engles and Genetti (1984) found blue blossom scrub in dense stands reaching a height of three meters, and different associates depending upon elevation. Its component shrubs are mostly typical of northern coastal scrub. Blue blossom is a temporary dominant in the canopy as a result of germination of seeds in a dormant seed bank of the soil after burning. After a long period free of burning, the cohorts released by disturbance become decadent and such sites then return to dominance by the typical shrubs of northern coastal scrub (Ford 1991).

Coffeeberry Scrub

In stands of this series, coffeeberry surpasses coyote brush in proportion of cover. At Point Reyes, Grams et al. (1977) found patches with canopies dominated by both coffeeberry and coyote brush in northern coastal scrub on the south-facing slopes in contrast to coyote brush dominance of the north-facing slopes. A distinct understory there had

affinities with southern coastal scrub. In contrast, Keeler-Wolf, Schindel, and San (2003) found coffeeberry dominating on north or northwest-facing moist slopes in Point Reyes National Seashore and Golden Gate National Recreation Area, which indicates a mosaic of differing patterns in that region. We have observed coffeeberry in greater abundance on north-facing slopes in Big Sur.

Poison Oak Scrub

In stands of this series, poison oak surpasses coyote brush in proportion of cover. Howell (1970:12) described patches of poison oak growing taller and denser on the moister north-facing slopes and as low bushes on the south-facing slopes within a landscape of scrub dominated by coyote brush in Marin County. The moister aspect factor appears to facilitate a reduction in coyote brush and favoring of poison oak in these patches (Keeler-Wolf, Schindel, and San 2003).

Hazel Scrub

This series is normally classified as a coniferous forest of the Coast Ranges and Sierra Nevada that has a distinctive understory of hazelnut *(Corylus cornuta* v. *californica)*. However, on some coastal slopes with unusually frequent exposure to marine fog and salt-laden cool air (e.g., Montara Mountain, the Marin Headlands, and Point Reyes), northern coastal scrub intergrades with hazelnut- and *Holodiscus discolor*-dominated stands (Vasey 2001; Vasey personal communication; Keeler-Wolf, Schindel, and San 2003). Vasey hypothesizes that this association is a relict of an Arcto-Tertiary mixed hardwood-conifer forest.

Composition

Sawyer and Keeler-Wolf (1995; personal communication) provides lists based on expert opinion and limited surveying of the shrub species most important in each series of northern coastal scrub (Table 7.2). Coyote brush occurs in all nine series with 24 additional shrubs of less frequency. The next most frequent shrubs are poison oak in six series, California sagebrush in five, and yellow bush lupine in five.

Nine of the 30 associations (30%) in Table 7.1 are designated with an asterisk as "rare and worthy of consideration" (CDFG 2003). This high level of rarity is associated with the narrow band of available habitat for the coastal bluff and wetland margin associations, the high diversity of habitat conditions generally, and habitat shifts that disfavor the associates of coyote brush due to natural succession (including increased extent, height, and canopy density of scrub stands that shade the understory in the long-term absence of fire and grazing disturbance).

Seventeen taxa with special-status designations occur within or in the vicinity of northern coastal scrub in the Coast Ranges between Santa Barbara and Del Norte counties (Table 7.3).

Landscape Dynamics

Northern coastal scrub is one of the major vegetation types in the network of open spaces, parks, ranchlands, and other rural wildlands of the Californian Coast Ranges and its dynamic succession relationships demand management. Suburban sprawl has removed much of this vegetation, and the habitat values of the remnants have been changed or diminished. Where northern coastal scrub has remained, it matures to dense tall stands and commonly encroaches into coastal prairie and annual grassland after natural disturbances are terminated. Release from frequent burning and livestock grazing has occurred where sprawl has fragmented the landscape, and where changed ownerships or culture now favor preservation with little deliberate vegetation management. As a result, northern coastal scrub is expanding in unmanaged areas at the wildland–urban interface; however, the total area is declining rapidly (Table 7.4). Thus fire hazards have increased within scrub stands and in the landscape as a whole. Prehistoric and historic characteristics of the rural grassland and oak savanna landscapes are giving way to scrub. Where scrub has expanded or matured, habitat quality has declined for special-status plants and animals dependent on the open grassland and mid-seral scrub. Habitat quality has also suffered from the concurrent effects of habitat fragmentation and urban influences, such as increased predation from domestic and feral pets, increased introductions of pest plants, and reduced water quality and stream flow.

The control of scrub encroachment and fire hazards and the maintenance or improvement of open grassland habitat qualities commonly require the mimicking or substitution of disturbance processes that occurred in the past, such as grazing and burning. In many cases, these management options have been neither feasible nor acceptable to the public or management agencies. Meanwhile the fire hazards and reduced habitat and aesthetic qualities are growing problems. Greater attention to northern coastal scrub vegetation is evident in the scientific literature since the 1970s, and since publication of the first edition of this book in 1977. Nevertheless, professional resource managers and the public need more information about its ecology and management to achieve our conservation goals.

PALEOHISTORIC AND HISTORIC LANDSCAPES

Axelrod (1988) suggested that interpretations of the paleohistory of northern and southern coastal scrub must be inferred from studies of other community types (because fossils of these soft-leaved shrubs are rare) and from ecological studies of the modern taxa that contribute to them. Such inferences seem reasonable, considering the great overlap in species distribution of most of these shrub species among California shrub and forest vegetation types. Axelrod (1989) emphasized the importance of frequent fire and summer drought in the evolution and ecology of California chaparral and coastal scrub vegetation types and their origins as generalists in previously more continuous forest cover. Northern

TABLE 7.2
Shrubs that Dominate the Canopies of the Nine Principal Series of Northern Coastal Scrub

		Series (Sawyer and Keeler-Wolf 1995; Natural Diversity Data Base: CDFG 2003)[1]								
Scientific Name	*Common Name*	NCBS	CSS	CBS	YLS	SHS	BBC	COS	POS	HS
Artemisia californica	California sagebrush	✓	✓	✓				✓	✓	
Artemisia suksdorfii	Coast mugwort					✓				
Baccharis pilularis	Coyote brush	✓	✓	✓	✓	✓	✓	✓	✓	
Ceanothus thyrsiflorus	Blue blossom			✓			✓			
Carpobrotus spp.	Ice plant	✓								
Dudleya spp.	Bluff lettuce	✓								
Encilia californica	California encilia		✓							
Ericameria ericoides	Heather goldenbush				✓					
Erigonum parvifolium	Coastal buckwheat	✓								
Eriodictyon spp.	Yerba santa		✓	✓						
Eriophyllum staechadifolium	Seaside woolly-sunflower	✓		✓		✓				
Garrya elliptica	Coast silktassel					✓				
Corylus cornuta v. californica	Hazelnut									✓
Gaultheria shallon	Salal			✓		✓	✓			
Holodiscus discolor	Ocean spray			✓						✓
Lotus scoparius	Deer weed		✓	✓						
Lupinus arboreus	Yellow bush lupine	✓		✓	✓	✓	✓			
Mimulus aurantiacus	Sticky monkeyflower		✓	✓		✓				
Myrica californica	Wax myrtle			✓	✓					
Rhamnus californica	Coffeeberry			✓				✓	✓	
Rubus parviflorus	Thimbleberry					✓				
Rubus spectabilis	Salmonberry					✓				
Rubus ursinus	California blackberry			✓		✓				
Toxicodendron diversilobum	Poison oak		✓	✓		✓	✓	✓	✓	
Vaccinium ovatum	Black huckleberry					✓	✓			

[a]Refer to Table 7.1 for Series codes; additional sources are cited in the text in the discussions of each series.

coastal scrub probably derived repeatedly from other communities and remains invasive and plastic in the landscape depending on fluctuating fire and climate regimes.

Northern coastal scrub species first appeared in California during the Miocene Epoch (26 to 5 million years before present [BP]) in North Coast forest and oak woodland, probably as understory, or in Miocene seral or xeric chaparral or coastal sage shrublands (Raven and Axelrod 1978; Axelrod 1988). They later appeared during the Pliocene Epoch (7 million years BP) in mixed evergreen forest. The Pliocene mountain uplifts apparently changed the burning conditions to favor scrub, as did continuation of climate drying in the Pleistocene. As the drying occurred, the woodland and forest types were segregated and confined, and the tree canopy disappeared from many areas, leaving the understory shrubs to dominate. The moderating marine climate along California's coast acted as a refuge, in a sense replacing the moderating effects of the once-present tree canopy.

TABLE 7.3
Special-status Plants of Northern Coastal Scrub or Vicinity (CNPS 2005)

Scientific Name	*Family*	*Occurrence*[a]	*CNPS*[b]	*State*[c]	*Federal*[d]
Astragalus tener var. *titi*	Fabaceae	Coastal bluff scrub, coastal prairie, GV, CCo, SnFrB	1B	CE	FE
Berberis pinnata ssp. *insularis*	Berberidaceae	Coastal scrub, ChI	1B	CE	FE
Cirsium occidentale var. *compactum*	Asteraceae	Coastal scrub and coastal prairie, CCo	1B	n/a	n/a
Cirsium rhothophilum	Asteraceae	Coastal bluff scrub, s CCo	1B	CT	n/a
Clarkia franciscana	Onagraceae	Coastal scrub, valley grassland, serpentine, SnFrB	1B	CE	FE
Delphinium bakeri	Ranuculaceae	Coastal scrub, n SnFrB, n CCo	1B	CR	FE
Delphinium luteum	Ranuculaceae	Coastal scrub, coastal prairie, moist cliffs, n CCo	1B	CR	FE
Dudleya gnoma	Crassulaceae	Coastal bluff scrub, ChI	1B	n/a	n/a
Dudleya nesiotica	Crassulaceae	Coastal bluff scrub, coastal scrub, ChI	1B	CR	FT
Dudleya traskiae	Crassulaceae	Coastal bluff scrub, coastal scrub, steep slopes, ChI	1B	CE	FE
Galium buxifolium	Rubiaceae	Coastal bluff scrub, coastal scrub, rocky, ChI	1B	CR	FE
Lessingia germanorum	Asteraceae	Coastal scrub, sandy, SnFrB	1B	CE	FE
Lilium occidentale	Liliaceae	Coastal bluff scrub, coastal scrub, coastal prairie, n NCo, sw OR	1B	CE	FE
Potentilla hickmanii	Rosaceae	Coastal bluff scrub, vernally wet meadows, n&c CCo, s NCoRO	1B	CE	FE
Sanicula maritima	Apiaceae	Coastal prairie, valley grassland, wet meadows and ravines, CCo, SnFrB	1B	CR	n/a
Stellaria littoralis	Caryophyllaceae	Coastal bluff scrub, coastal scrub, moist, NCo, CCo	1B	n/a	n/a

[a]Occurrence (CNPS 2005; Hickman 1993): CCo = Central Coast; ChI = Channel Islands; GV = Great Central Valley; NCo = North Coast; NCoRO = Outer North Coast Ranges; OR = Oregon; SnFrB = San Francisco Bay.
[b]CNPS Codes: 1B = Rare, threatened, or endangered in California and elsewhere.
[c]State Codes: CE = California endangered; CT = California threatened; CR = California rare.
[d]Federal Codes: FE = Federal Endangered; FT = Federal Threatened.

TABLE 7.4
Approximate Area of Northern Coastal Scrub

Year	*Area (Hectares)*[a]	*Area (Acres)*[a]	*Change Since 1950*
1950	623,600	1,559,000	0%
1980	587,200	1,468,000	−5.8%
2001	397,200	993,000	−36.3%

[a]Represents the "North Coast" and "Central Coast" areas of "Coastal Scrub" vegetation (FRRAP 1988,Table 7-4; FRAP 2003, Chap. 2, Table 1); 2001 estimates of north and central areas based on average proportions reported for 1950 and 1980.

TABLE 7.5
Shrubs of Northern Coastal Scrub that Occur in Other Major Vegetation Zones

	Major Vegetation Zone			
Shrub Species	Conifer Forest	Closed-Cone Pine Forest	Woodland-Chaparral	Arid Tropic Scrub /Semidesert
Artemisia californica			✓	✓
Baccharis pilularis				✓
Ceanothus thyrsiflorus		✓		
Corylus cornuta	✓			
Dudleya spp.				✓
Eriophyllum stachaedifolium			✓	
Gaultheria shallon		✓		
Lotus scoparius			✓	
Lupinus arboreus			✓	
Mimulus aurantiacus			✓	
Rhamnus californica			✓	
Toxicodendron diversilobum	✓			
Vaccinium ovatum		✓		

NOTE: From Axelrod (1978, Table 2).

Coastal sage and chaparral spread widely as a result of the elimination of summer rain when the Mediterranean climate became more severe, but coastal sage developed after chaparral (Axelrod 1978) and in a zone lower in elevation and drier than the chaparral zone.

Axelrod (1978) suggests the origins of the component shrubs of northern coastal scrub may be inferred from their occurrence in other major vegetation zones (Table 7.5).

A pollen record study from sediment cores at Laguna de las Trancas in northern Santa Cruz County by Adam, Byrne, and Luther (1981) indicated no recognizable coyote brush, California sagebrush, or other shrubs of northern coastal scrub or chaparral in the oldest stratum (24,000–30,000 years BP); high proportions of huckleberry, salal, and grass pollen in the next younger stratum (12,000 to 24,000 years BP) and a glacial period climate similar to the present; and possible but unrecognizable pollen from chaparral shrubs in the most recent stratum (5,000 to 12,000 years BP). This suggests that salal-black huckleberry scrub was present farther south of its current range during the Upper Wisconsinan full glacial advance during the Pleistocene. This study is not conclusive about when other shrubs of northern coastal scrub arrived to this area.

Since the Miocene, wildfires in the coastal mountains of the Monterey Bay were primarily ignited by lightning and burned extensively in mixed evergreen and redwood forests on the mountaintops (Greenlee and Langenheim 1990). They estimated that mean fire intervals in these forests were 30–135 years. Consequently, only incidental burning occurred in coastal prairies, coastal scrub, chaparral, and oak woodlands in lower elevations, with mean intervals of up to 15 years in prairie and scrub and 30 years in chaparral and woodland.

We speculate this lightning fire regime resulted in extensive scrub cover on the coastal terraces and hills prior to arrival and frequent burning by the California Indians. As such, northern coastal scrub might have been relatively more common then than it is currently, and coastal prairie confined to smaller areas than occur today. In many places near the coast Douglas fir and other conifers commonly colonize and shade out patches of northern coastal scrub; and similarly oak-bay woodland commonly colonizes scrub at more inland sites. Inferring from this ecological evidence, we speculate that forest and woodland cover might have been most common, and that northern coastal scrub might have occurred mostly in the more wind-swept and salt-laden areas near the coast, or as seral patches on landslides, burns, and other disturbance areas, which precluded a cover of forest or woodland.

Native mammalian grazing (including by the megafauna that became extinct in the Pleistocene) was probably very important in maintaining open prairie and reducing brush and tree encroachment prior to the arrival of the California Indians (Edwards 1996). The grazing behavior of the extinct

mammals and large free herds of the extant animals is not well understood, but is assumed to have caused severe defoliation and trampling to both herbaceous and woody forage. We speculate that such grazing pressure was patchy and did not occur everywhere that the shrub vegetation occurred. Thus the resulting effects on shrubs would have been quite variable in severity and extent over time, including development and persistence of mid- and late-succession shrub refugia.

Periodic drought was also important. Droughts plus grazing might have caused the relative proportions of prairie, scrub, and succession to forest to fluctuate with herbivore populations and drought cycles over long periods.

Burning of coastal brush by California Indians before Spanish colonization is accepted. However, plant cover, burn timing, and other conditions are not well known. Lewis (1993) reports numerous northern coastal scrub species that can occur as a forest understory, and that Indian burning could have been directed to clearing such brush from the landscape. Burning was conducted repeatedly to improve hunting of game and grass seed production. Keeley (2002) suggests that intact shrublands would have provided limited resources for native Californians; thus there was ample motivation to burn the woody vegetation and convert it to a mosaic of scrub and grassland, which would have been more valuable.

Father Juan Crespi (reported in Paddison 1999), documented a 1769 Spanish expedition with the explorer Portola to San Francisco Bay. Crespi describes "very grassy hills" and "high big hills all covered with good soil and grass—though almost all the grasses had been burned" and hazelnut trees in the creeks on the coast side and ridges. He describes hills "grown over" with oak groves and wide flat land with good black, very grassy soil, all burned, under the oaks with less fog on the bay side. Unburned places provided "abundant pasture." His early accounts suggest a smaller cover of scrub on the coastal terraces and hills than today, and frequent burning of the grasslands by the California Indians. The diaries of Ensign Miguel Costanso (reported in Browning 1992) provide another account of the same expedition and reveal the presence of dense brush in gullies, on stream channels, and river bottoms. The expedition's travel across hills "covered with pasture" burned by the natives was frequently interrupted for brush clearing. This account suggests that riparian brush could have been composed of *Salix* species, but there is no clear indication whether the gullies might have included coastal scrub.

Gordon (1985) states these terraces and hills were maintained in grass cover with minimal woody invasion or establishment of scrub by the prolonged burning practices of the Costanoan Indians. We speculate that northern coastal scrub species would have been confined to forest understories, gullies, eroded or rocky hillsides, or other places less prone to burn with the frequent grass fires in the landscape of the California Indian era. Thus, with grazing by the Pleistocene megafauna absent, the northern coastal scrub could have been *un*confined only in places where the Indians did not practice repeated burning, such as far from settlements or very steep slopes.

Since the beginning of the Spanish-Mexican era, these open grasslands have been maintained by extensive livestock grazing coupled with increased deer browsing (due to increasing deer populations associated with declining predator populations (Dasmann 1981, 14) in addition to drought and soil limits. After many millennia without grazing by the Pleistocene Megafauna, the Spanish and Mexican colonists returned a major ungulate grazing effect on California coastal vegetation with the introduction of livestock grazing. Its effects on northern coastal scrub were probably similar to the burning and native grazing of the past, with an important exception. Domestic cattle grazing on the coast has been more uniform in extent and severity of effects throughout the grazed areas each year than the native pre-historic migratory ungulates apparently were. At the same time, the native prairie plant composition shifted to mostly European annuals, with unknown consequences to grazing behavior and shrub–herb interactions. More recently, exclusion of livestock grazing and wildfires from the coastal terraces and hills of Central California has resulted in the loss of extensive grasslands and the encroachment of northern coastal scrub.

Reports from early American explorers and botanists confirm the extent of coastal grasslands free of brush (reviewed in Dasmann 1981, 24–26; Burcham 1957). Edwards (2002) dramatically illustrated this point with photographs of the East Bay Hills from the early 1900s and about 100 years later. Open grasslands with restricted zones of riparian woodland and scattered scrub on north-facing slopes has converted to dense coyote brush scrub and mixed forest with only remote patches of grassland.

MODERN LANDSCAPES

Coyote Brush *(Baccharis pilularis)*

Areas free of abundant annual grasses, including "bare zones" (due to rodents, shading, allelopathy, and precipitation), landslides, and grazing-exposed soil, provide more favorable sites for the establishment of coyote brush due to the reduction of grass interference (McBride 1964; McBride and Heady 1968; da Silva and Bartolome 1984). Coyote brush invades grassland by means of seed dispersal and establishment. McBride (1964) found the amounts of seed diminished with distance from the edge of the existing shrubs, and no difference in dispersal of seed was observed up or down hill. The invasion into grassland was mainly at stand edges in bare zones, moving uniformly, not scattered, possibly because of the presence of grazing livestock and deer.

Da Silva and Bartolome (1984) found that coyote brush seedlings initially grow slower than their typical annual grass associate seedlings, but produce long taproots, which can endure the drought of the first summer if that root

reaches adequate soil moisture. *Bromus hordeaceus* seedlings suppressed adjacent coyote brush seedlings, especially where there was low soil moisture. The conditions most favorable for coyote brush establishment are summer coastal fog, greater than average precipitation, and late rains, which reduce moisture stress. Conditions unfavorable for coyote brush establishment are early rains, lower than average precipitation, and drier sites, which favor grass domination before the coyote brush seed disperses and plants establish (Williams and Hobbs 1989). Coyote brush summer mortality is also caused by severe soil cracking (McBride 1964; McBride and Heady 1968). Coyote brush seedling growth is limited where shaded (McBride 1974). Once established, coyote brush adults are not limited by moisture (Wright 1928).

The presence of coyote brush scrub in a grassland matrix can facilitate the establishment of mixed woodland at the same site by providing protection from browsing by cattle and wildlife as well as from water and temperature stress. Callaway and D'Antonio (1991) found that 80% of coast live oak seedlings were under shrub canopies whether or not grazed by livestock, and 31% of plantings survived under shrubs compared to 0% in the open.

Blue Blossom *(Ceanothus thyrsiflorus)*

Blue blossom reproduces from seed. It is killed by even light fires, because it is a nonsprouter. Following fire, it regenerates only from seed germination and seedling establishment. We have reviewed fire history maps of Big Sur and found sites with decadent blue blossom that burned more than 44 years ago, which suggests this species responded to the burn with synchronous germination and establishment from seeds in the soil seedbank. At these sites, the 44-year-old cohort had reached a natural senescence and was dying. We also found sites where no blue blossom was known prior to burns (Ford 1991). This effect was also noted at the site of the 1995 Mount Vision fire in Point Reyes National Seashore by David and Parker (1997) and Keeler-Wolf, Schindel, and San (2003).

Yellow Bush Lupine *(Lupinus arboreus)*

Davidson and Barbour (1977) found that *Lupinus* seedling establishment was limited by competition with grass for light, moisture, loss to herbivores, and drought desiccation, but not allelopathy. They also reported that low grass cover, seed burial by rodents, exposure to heating and cooling, wetting and drying, and salt aerosols each enhanced *Lupinus* germination. Germination competition between the *Lupinus* seedlings can reduce the eventual density of established stands (Pickart and Sawyer 1998).

FIRE ECOLOGY

Fire regimes in northern coastal scrub changed with arrival of the California Indians at the end of the Pleistocene, notably the increased frequency and shift in location of ignitions from the upper-elevation mountain forests to the lower elevation coastal prairie, coastal scrub, and oak woodland (Greenlee and Langenheim 1990). This reflects the shift from lightning ignitions to California Indian ignitions.

The Indians practiced frequent burning until the 18th century (Lewis 1993). Subsequently, burning has been suppressed. Historical records and recent observations of brush invasion of coastal grasslands (McBride and Heady 1968) suggest that coyote brush scrub was less extensive within its range during California Indian and early Spanish colonial periods than it has been recently. Therefore, many coyote brush scrub stands found today appear to represent varying stages of development since invasion during the last 200-plus years.

McBride (1974) found that exclusion of wildfire from the East Bay Hills resulted in increased survival of coyote brush seedlings in the grassland matrix as well as coast live oak and bay laurel *(Umbellularia californica)* saplings in the scrub matrix. With recurrent fire in those landscapes, the grasslands were maintained with less scrub invasion, and the coyote brush stands were maintained with less tree invasion. In the Potrero Hills of the East Bay Area, Havlik (1984) found that short intervals between burns reduced coyote brush survival, and that otherwise it returned to its former relative cover in three years. Fire-return intervals of less than 3 years reduced coyote brush survival.

Like other shrub types that grow in California's Mediterranean-type climate, northern coastal scrub develops a high fire hazard due to the dense accumulation of great quantities of woody fuel and long periods of dry weather. Frequent, high-intensity, canopy-consuming wildfires are common. Estimates of prehistoric and historic fire-return intervals and their extent in northern coastal scrub landscapes are uncertain. However, Greenlee (1983) and Greenlee and Hart (1980) estimated fire intervals of 1 to 10 years where associated with Indian and early settler grassland burning, 20 to 30 years in pure brush areas, and 20 to 100 years in brush mosaics with woodlands that are subject to lightning ignitions.

The mortality of individual coyote brush plants from fire is greater when the bases are burned and the fire is more severe (McBride and Heady 1968; Ford 1991). McBride and Heady (1968) found that controlled burning of coyote brush adults resulted in greater mortality with simulated basal burning than with simulated crown-only burning. Basal burns were facilitated by herbaceous understory fuels. Ford's Big Sur study (1991) found the same result for two other postfire sprouting shrubs of northern coastal scrub: coffeeberry and poison oak. All three of these shrubs resprouted readily after fire, even after extremely severe, high-intensity fires. He found that the nonsprouting obligate seeders blue blossom, seaside woolly-sunflower, and deerweed *(Lotus scoparious)* were mostly killed by any severity of fire, and regenerated from seeds in the soil seed bank. Where deerweed was subject to light severity fire, fewer seedlings were found. Two shrubs that can regenerate from both sprouts and seeds, California sagebrush and sticky monkey flower, exhibited a

regeneration pattern similar to that of the obligate seeders. At Point Reyes, David and Parker (1997) also reported the dramatic appearance of blue blossom after fire in a northern coastal scrub site that had last burned long enough in the past for adults to senesce and disappear.

GRAZERS

McBride (1974) found that cattle and deer browsing results in the uprooting, defoliation, and trampling of coyote brush seedlings in grasslands of the East Bay Hills. Coyote brush is one of few green browse plants available during the dry seasons, so this effect is more common in the summer and fall when the herbaceous forages are relatively less palatable. Where grazing and fire are removed from these landscapes, coyote brush scrub invades and overtakes the grassland. There was no significant expansion or establishment of coastal scrub into coastal prairie after 6 years exclusion of livestock grazing at Pt. Reyes (Elliott and Wehausen 1974). Keeler-Wolf (personal communication) speculated that this relates to the more severe coastal climate near the coast as opposed to less severe climate where scrub colonization is more common, such as in the East Bay Hills. The denser sod of perennial grasses would also be less likely to afford good germination sites for colonizing coyote brush.

Like excessive livestock grazing, rodent herbivory can contribute to bare zones in coyote brush scrub. McBride (1964; McBride and Heady 1968) found this add sites for coyote brush seedling colonization. Coyote brush seedling survival increased when rodents and cattle were excluded (more so than cattle exclosure only and no exclosure).

In yellow bush lupine scrub, Davidson and Barbour (1977) found significant seedling and adult mortality caused by insect larvae herbivory and summer drought. Rodents consumed most of the lupine seedfall and seedlings, but cached seeds in their burrows, which enhanced the stand's future germination success. These rodent activities cause fluctuations in the spacing and age-class structure of the Lupine scrub.

SUCCESSION

Frequent fire, rodent herbivory, livestock grazing and trampling, and drought tend to maintain grassland and limit succession from grassland to northern coastal scrub as well as the succession from scrub to mixed oak woodland (McBride 1974; Williams, Hobbs, and Hamburg 1987) and to bay laurel woodland in the San Francisco Bay Area (Safford 1995). Holland and Keil (1995, 158) reported coyote brush succession to conifers at the northern edges of the coyote brush range. Belsher (1999, 55) suggested that human disturbance maintains coyote brush, salal, and blue blossom in Humboldt and Del Norte counties but once released, succession proceeds to Sitka spruce *(Picea sitchensis)*. Keeler-Wolf, Schindel, and San (2003) described Douglas fir colonizing coyote brush at Point Reyes National Seashore and the Golden Gate National Recreation Area. We have observed coyote brush scrub being colonized by Douglas fir and Monterey pine *(Pinus radiata)* on the coasts of Santa Cruz and San Mateo counties.

McBride and Heady (1968) found that coyote brush scrub had expanded into grassland at the average rate of 18.4 ha per year between the 1920s and the 1960s, or an average increase in brush area of about 5.2% (of the original 220 ha area) per year, after livestock grazing was terminated. They estimated that succession from coyote brush scrub to woodland, in the absence of recurrent fires, would require at least 50 years. At Jasper Ridge, coyote brush scrub colonization into grassland was restricted to distinct pulses, characterized by higher temperatures and rainfall in the late spring (Williams, Hobbs, and Hamburg 1987; Williams and Hobbs 1989). At Big Creek Reserve in Big Sur, about 42% of former grassland was replaced by coastal scrub between 1932 and 1982 (Engles and Genetti 1984). This represents an average grassland conversion of about 3.0 ha per year, or about 0.8% (of the original 355 ha area) per year, despite livestock grazing. A follow-up study in the East Bay Hills by Russell and McBride (2003) demonstrated that the conversion of grassland to scrub continued for another 30 years (after the 1970s) and that fuel loads increased, contributing to an increased probability of high intensity wildfire.

Havlik (1984) described two additional successional pathways for short-lived coyote brush plants in the Potrero Hills: (1) grass to brush in a grassland matrix and return to grassland; and (2) grass to brush to decadent brush, and return to grass. Soil quality can effect whether the coyote brush stagnates or reverts to grassland after invasion without fire. Coyote brush canopies closed and herbaceous species cover declined dramatically after three years in recently invaded grasslands of eastern San Mateo County (Hobbs and Mooney 1986). Coyote brush canopies collapsed and most individuals died after nine years. Then a new cycle commenced with coyote brush seedling growth, canopy closure, and decadence again.

Hobbs and Mooney (1985) measured stump re-sprouting after top removal from different ages of coyote brush individuals at Jasper Ridge. Sprouting (stem length and leaf number) was progressively greater in plants between 1 and 4 years old when cut, then declined to no re-sprouting for plants 9 years old. This decline was attributed to inactivation and engulfment of regrowth buds by thick secondary growth. In contrast, burned coyote brush plants of much greater age (44 + years) resprouted vigorously from bases and stems after fire at Big Sur (Ford 1991). Coyote brush plants from two inland regions (Potrero Hills and Jasper Ridge) apparently differed in regrowth potential from those of Big Sur. Alternatively, fire might have stimulated reactivation of old inactive buds; and older plants might have developed active buds on buried stems or lignotubers.

As noted earlier, McBride (1974; McBride and Heady 1968) suggested that the greatest coyote brush mortality occurred where basal burning was fueled by an herbaceous understory. Basal burning would be limited by coyote brush

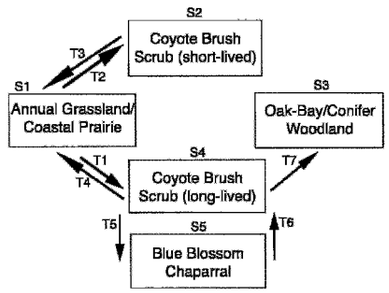

FIGURE 7.4 Diagram of coyote brush scrub succession (arrows indicate transition directions between states in boxes).

FIGURE 7.5 A stand of coastal prairie within a scrub-grassland mosaic in Humboldt Co. Photo courtesy of Harold Heady.

scrub's sparse understory in its southern range. High shrub mortality and low regeneration or reproduction would be necessary to convert southern stands to an earlier successional grassland community. Most fires in coyote brush scrub do not appear to achieve such effects. However, California Indian and early settler management practices must have confined scrub and enlarged grassland areas, according to historical landscape assessments.

Succession in coyote brush scrub may be appreciated best in a generalized model representing the states and transitions of the succession sere described above (Fig. 7.4).

Coastal Prairie

Coastal prairie is a much-altered herbaceous community blanketing hills and terraces and framing California's famous coastal vistas (Fig. 7.5). The distinction between coastal prairie and other types of Californian grasslands (desert, montane, valley, savannah, etc.) is covered elsewhere in this volume. Urban and agricultural development, succession to woody plant communities, and weed invasion are principle threats. As with northern coastal scrub, management is required for the maintenance of species richness, and yet active management for the habitat on protected lands is largely unpracticed.

Classification and Locations

Undoubtedly, Native Californians were the first to describe, recognize, interact with, and manage California's coastal prairie. Village and shell mound sites are frequently found adjacent to remaining coastal prairie areas and, interestingly, appear correlated with the most intact remaining examples of this habitat type. What little was recorded of Native Californian ethnobotany provides a long list of important species from coastal prairie (Stodder 1986). Indeed, the extensive management by these peoples is probably responsible for maintaining most large areas of grassland along the coast up to the time of contact with Old World Peoples (Gordon 1985). Because of the rapidity of their conquest, no detailed account remains describing the uses and management of this habitat type.

The earliest accounts of California's coast noted the extensive grasslands, especially in eastern San Francisco Bay and near Monterey. Because of their interest in pastoral production, early explorers who described coastal prairie naturally noted an abundance of native perennial grass species (Heady et al. 1977). Ranchers in the 1820s recognized coastal prairie areas as more productive than all but the most mesic Central Valley grasslands; as a result, most cattle and sheep ranching was focused in areas of coastal prairie (Burcham 1957). Botanical descriptions from the late 1800s noted the predominance of native perennial grasses, grasses that were described as providing extremely good forage in the coastal grasslands of Santa Cruz County (Harrison 1890), and other locations.

In recent decades, coastal prairie has increasingly gained recognition by ecologists as a community separate from other grassland types. Two major Californian grassland types, valley grassland and coastal prairie, were originally differentiated on the basis of climate, dominant grass species, and affinities of the vegetation with southern or northern bioregions (Burcham 1957; Munz and Keck 1959). These distinctions remain important to interpret these community types, although their separation seems forced in areas where the gradient of maritime influence is gradual and spread over large geographic areas.

Burcham (1957) may have been the first to coin the term "coastal prairie" in published literature, noting that it occurred patchily, especially in Humboldt and Mendocino Counties, but extended as far south as Marin County. He mapped extensive areas of grassland farther south, in San Luis Obispo and Santa Barbara Counties, but he described these as "valley grassland."

Küchler (1964) used expert opinion to map generalized areas of coastal prairie, which he termed a "fescue-oatgrass *(Festuca-Danthonia)*" community. Although Küchler included large areas not mapped by Burcham (1957), he agreed in general that the coastal prairie began north of San Francisco

Bay on the western slopes of the Coast Ranges, and that it continued up the coast into southern Oregon. His map work identified 355,614 ha as originally covered by *Festuca-Danthonia* grassland. Recent studies indicate that at least 24% of his mapped unit (85,347 ha) has been urbanized, the largest percentage of any major plant community type in the United States (Loveland and Hutcheson 1995). These figures do not include the extent of the original habitat or its destruction south of the San Francisco Bay.

In the early 1970s, a survey of grasslands conducted by the California Department of Parks and Recreation State Parks extended the range of coastal prairie southward to Pt. Lobos State Reserve, near Monterey (Barry 1972). The report also suggested that the valley grassland type extended into coastal areas of Marin, Monterey, and San Luis Obispo Counties. Unfortunately, this and other community descriptions through the early 1970s were not based on quantitative data, but on anecdotal information about common species (Table 7.6). However, research from the mid-1970s onward provided quantitative data on the composition of this community, suggesting that coastal prairie maps should include all coastal grasslands from San Francisco Bay south to Monterey Bay (Elliot and Wehausen 1974; McBride 1974; Schlinger et al. 1977).

The most recent research suggests extending the range for coastal prairie even to include areas of San Luis Obispo County (Stromberg et al. 2002). Parts of Los Angeles County have been proposed as historically another type of native annual forb dominated coastal prairie, including bicolored lupine *(Lupinus bicolor)*, California sun cup *(Camissonia bistorta)*, Brand's Phacelia *(Phacelia stellaris)*, hairy lotus (*Lotus strigosus*), etc. (Longcore and Mattoni 1997). California coastal prairie has its evolutionary origins associated with the northern Pallouse prairie. This is especially evident with northern relict species such as *Deschampsia caespitosa*, *Danthonia californica*, *Calamagrostis nutkaensis*, and a number of Carex species commonly found in coastal prairie. However, a number of species also commonly found in coastal prairie may have evolutionary affinities with more southern biomes: species of tarweeds *(Hemizonia, Madia*, and *Holocarpha)*, *Linanthus*, and *Lupinus*.

The range of coastal prairie vegetation associations is clearly tied to proximity to the coast and marine influences, as well as topographic position; it is contained within the bounds of the distribution of northern coastal scrub as illustrated in Fig. 7.2. At this time, we believe that the more species-rich grasslands are in moister areas with more maritime influence; as more plot-based data are collected, we will gain a greater appreciation for species distribution trends as affected by edaphic factors, further refining the distribution map.

An analysis of the data combined from the research presented in Hayes and Holl (2003) and Stromberg (2002) suggests that there are roughly three major vegetation types of coastal prairie (Table 7.7). Analysis used individual plot and transect from the original datasets, separated by TWINSPAN and modified by Ayzik Solomeshch. The titles of each of the vegetation types are based on the closest approximation to series names given by Sawyer and Keeler-Wolf (1995).

CALIFORNIA ANNUAL GRASSLAND

Ripgut brome *(Bromus diandrus)* and wild oat *(Avena fatua)* define a second major coastal prairie type (Table 7.7, columns 1–2). Many areas of rich-soiled coastal prairie are currently dominated by a mixture of annual plants, mostly exotic grasses and forbs; Common dominant forbs include Italian plumeless thistle *(Carduus pycnocephala)*, milk thistle *(Silybum marianum)*, and short pod mustard *(Hirschfeldia incana)*. Native perennial species are sparse, although purple needlegrass and native shrubs are found. We suggest that the low proportion of natives in these communities is because these areas may be "old fields," areas that have been previously cultivated. The common grass and forb dominants significantly overlap with those found in Central Valley grasslands, and it is not difficult to find this type of grassland nearly anywhere in California, but a few areas that would be classified as this grassland type may still contain important native plant assemblages either above ground or below ground.

CALIFORNIA OATGRASS

California oatgrass is probably the most important native grass species in the grasslands of many of the mesic, rich soiled coastal terrace grasslands (Table 7.7, columns 3–9). California oatgrass is classified as a wetland indicator species "facultative wetland species" by the U.S. Fish and Wildlife Service (USFWS) in California (1996). Three subtypes of the California oatgrass community were found in the analysis.

First, the most common type found also contains an extraordinary variety of native perennial species as well as exotic annuals (Table 7.7, columns 3–4). California brome grass *(Bromus carinatus)* and purple needlegrass were quite frequent. Common forbs included California buttercup *(Ranunculus californicus)* as well as the nonnative English plantain *(Plantago lanceolata)*, cut-leaved geranium *(Geranium dissectum)*, sheep sorral *(Rumex acetosella)*, sub clover *(Trifolium subterraneum)*, and bur clover *(Medicago polymorpha)*.

A second common California oatgrass community included tufted hairgrass *(Deschampsia caespitosa)* and coyote brush; this community was also found on rich, moist soils and, as with the first community, contained a large variety of native perennial and exotic annual plant species (Table 7.7, columns 5–7). Other important species included Douglas' iris *(Iris douglasiana)* and soap root *(Chlorogalum pomeridianum)*.

A third vegetation type, called in Sawyer and Keeler-Wolf (1995) "exotic perennial grassland," was indicated by hairy oatgrass *(Danthonia pilosa)* and various *Carex* species on moist, sometimes poor and acidic soils (Table 7.7, columns 8–9). In areas, other exotic perennial grass species dominate this community, including Kentucky bluegrass (*Poa pratensis*) and velvet grass *(Holcus lanatus)*, as well as (in a few areas) sweet vernal grass *(Anthoxan-*

TABLE 7.6
Published Species Lists for California Coastal Prairie

Scientific Name	*Common Name*	*Family*	*Location*
Munz and Keck (1959)			
Festuca idahoensis	Idaho fescue	Poaceae	North of SF
Danthonia californica	California oatgrass	Poaceae	Widespread
Calamagrostis nutkaensis	Pacific reed grass	Poaceae	
Deschampsia caespitosa	Tufted hairgrass	Poaceae	Widespread
*Holcus lanatus**	Velvet grass	Poaceae	Widespread
Pteridium aquilinum var. pubescens	Bracken fern	Pteridaceae	Widespread
Carex tumulicola	Foothill sedge	Cyperaceae	Widespread
Dichelostemma capitata	Blue dicks	Liliaceae	
Iris douglasiana	Douglas' iris	Iridaceae	North of SF
Sisyrinchium bellum	Blue eyed grass	Iridaceae	Widespread
Calochortus luteus	Yellow mariposa lily	Liliaceae	Widespread
Ranunculus californicus	California buttercup	Ranuculaceae	Widespread
Lupinus formosus	Summer lupine	Fabaceae	
Lupinus variicolor	Varied lupine	Fabaceae	Widespread
Sanicula arctopoides	Footsteps of spring	Apiaceae	Widespread
Heterotheca sessiliflora ssp. Bolanderi	Bolander's golden aster	Asteraceae	
Grindelia hirsutula var. *hirsutula*	Hairy gumplant	Asteraceae	Widespread
Kuchler (1964)			
Carex tumulicola	Berkeley sedge	Cyperaceae	Western slopes of northern Coast Ranges, California
Danthonia californica	California oatgrass	Poaceae	"
Deschampsia caespitosa	Hairgrass	Poaceae	"
Agrostis hallii	Hall's bentgrass	Poaceae	"
Dichelostemma capitata	Blue dicks	Liliaceae	"
Calamagrostis nutkaensis	Pacific reed grass	Poaceae	"
Heterotheca sessiliflora ssp. Bolanderi	Bolander's golden aster	Asteraceae	"
Grindelia hirsutula var. *hirsutula*	Hairy gumweed	Asteraceae	"
Iris douglasiana	Douglas' Iris	Iridaceae	"
Lupinus formosus	Summer lupine	Fabaceae	"
Lupinus variicolor	Varied lupine	Fabaceae	"
Pteridium aquilinum var. *pubescens*	Bracken	Pteridaceae	"
Ranunculus californicus	California buttercup	Ranunculaceae	"
Sanicula arctopoides	Footsteps of spring	Apiaceae	"
Sisyrinchium bellum	Blue-eyed grass	Iridaceae	"
Stipa lepida	Small-flowered needlegrass	Poaceae	"

TABLE 7.6 (continued)

Scientific Name	*Common Name*	*Family*	*Location*
Howell (1970)			
Deschampsia caespitosa	Tufted hairgrass	Poaceae	Widespread
Calamagrostis nutkaensis	Pacific reed grass	Poaceae	North of Carmel
Festuca californica	California fescue	Poaceae	Widespread
Juncus effusus	Common rush	Juncaceae	Widespread
Carex obnupta	Coast carex	Cyperaceae	Widespread
Camassia quamash var. *linearis*	Death camas	Liliaceae	Widespread
Brodiaea terrestris	Dwarf Brodiaea	Liliaceae	Widespread
Calochortus tolmiei	Pussy ears	Liliaceae	North of SF
Maianthemum dilatatum	Pacific May-lily	Liliaceae	
Sisyrinchium bellum	Blue eyed grass	Iridaceae	Widespread
Platanthera leucostachys	Pacific bog orchid	Orchidaceae	
Spiranthes romanzoffiana	Lady's tresses orchid	Orchidaceae	North of Carmel
Polygonum bistortoides	Snakeweed	Polygonaceae	
Claytonia sibirica	Candy flower	Polygonaceae	
Stellaria littoralis	Seaside chickweed	Caryophyllaceae	North of SF
Ranunculus californica	California buttercup	Ranuculaceae	Widespread
Delphinium decorum	Coast larkspur	Ranuculaceae	
Sidalcea malvaeflora	Checkerbloom	Malvaceae	Widespread
Viola adunca	Western dog violet	Violaceae	North of SF
Clarkia amoena	Farewell to spring	Onagraceae	Endemic to Marin County
Lilaeopsis occidentalis	Western grasswort	Apiaceae	
Veronica scutellata	Marsh speedwell	Schrophulariaceae	
Triphysaria eriantha var. *rosea*	Johnny tuck	Schrophulariaceae	
Orthocarpus floribundus	San Francisco owl's clover	Schrophulariaceae	Endemic to Marin County
Plantago subnuda	Naked plantain	Plantaginaceae	
Campanula californica	California harebell	Campanulaceae	
Lessingia filaginifolia var. *californica*	California aster	Asteraceae	Widespread
Cirsium andrewsii	Franciscan thistle	Asteraceae	
Ornduff (1974)			
Heterotheca sessiliflora ssp. *Bolanderi*	Bolander's golden aster	Asteraceae	
Iris douglasiana	Douglas' iris	Iridaceae	North of SF
Pteridium aquilinum var. *pubescens*	Bracken fern	Pteridaceae	Widespread
Sanicula arctopoides	Footsteps of spring	Apiaceae	Widespread
Kozloff and Beidleman (1994)			
Calamagrostis nutkaensis	Pacific reed grass	Poaceae	

(continued)

TABLE 7.6 (continued)

Scientific Name	*Common Name*	*Family*	*Location*
Calochortus luteus	Yellow mariposa lily	Liliaceae	Widespread
Danthonia californica	California oatgrass	Poaceae	Widespread
Deschampsia caespitosa ssp. *holciformis*	Pacific hairgrass	Poaceae	Widespread
Dichelostemma congestum	Ookow	Liliaceae	
Festuca idahoensis	Idaho fescue	Poaceae	North of SF
Grindelia hirsutula var. *hirsutula*	Hairy gumplant	Asteraceae	
Heterotheca sessiliflora ssp. *Bolanderi*	Bolander's golden aster	Asteraceae	
Iris douglasiana	Douglas' iris	Iridaceae	
Lupinus formosus	Summer lupine	Fabaceae	
Lupinus variicolor	Varied lupine	Fabaceae	
Pteridium aquilinum var. *pubescens*	Bracken fern	Pteridaceae	Widespread
Ranunculus californicus	California buttercup	Ranuculaceae	Widespread
Sanicula arctopoides	Footsteps of spring	Apiaceae	Widespread
Sisyrinchium bellum	Blue eyed grass	Iridaceae	Widespread

NOTE: These published lists contain species thought to be "characteristic" of coastal prairie, not necessarily species that were dominant. Little or no data are referred to in conjunction with these lists, which appear to build on one another through time.

thum odoratum) tall fescue *(Festuca arundinacea)*, and Harding grass *(Phalaris aquatica)*.

MOIST NATIVE PERENNIAL GRASSLAND

Meadow barley *(Hordeum brachyantherum)*, brown-headed rush *(Juncus phaeocephalus)*, along with various *Carex* species are the native species that define a third major coastal prairie type, which is found on the moistest coastal prairie sites. Other co-dominant exotic species include curly dock *(Rumex crispus)* and hyssop loosestrife *(Lythrum hyssopifolia)*.

Research suggests that the divisions between inland grassland community types are edaphically controlled (Evans 1989; Dyer, Fossum et al. 1996), whereas disturbance may play a more crucial role in determining the composition of coastal grasslands (Hatch, Bartolome et al. 1999; Corbin and D'Antonio 2004). More research is needed in comparing the sometimes long-lasting seed banks (especially forbs, but some graminoids) of these habitat types to examine historical composition and/or potential vegetation composition.

Endemics, Near-Endemics, and Species of Concern

There are nearly 80 species of plants endemic to coastal prairie (Table 7.8). Although a few species can be found throughout coastal prairie, a mosaic of geographic and edaphic differences favor and sort different assemblages of species. Almost all coastal prairie communities, like most vegetation types in low-elevation California, are dominated by exotic species. Exotic annual grasses, perennial grasses, annual forbs, and perennial forbs will probably increasingly dominate coastal grasslands in the near future. Many of the coastal exotic taxa are also part of today's Central Valley grassland.

Because most of the historical coastal prairie has been floristically changed or destroyed, an increasing number of species have declined in population numbers such that they warrant listing as rare or endangered (Table 7.9). The number of coastal prairie native annual forbs that are considered rare and endangered is increasing, probably because of lack of appropriate disturbance regimes (Hayes and Holl 2003). These include *Holocarpha macradenia* and species of *Plagiobothrys, Triphysaria*, *Trifolium*, *Linanthus*, and *Limnanthes* (Howell 1970).

There are also a number of threatened native perennial grasses associated with coastal prairie, such as species of *Agrostis*, including the very rare *A. blasdalei* (Blasdale's bentgrass) and *A. aristiglumis* (Pt. Reyes bentgrass; Crampton 1974). The endangered *Alopecurus aequalis var. sonomensis* (Sonoma foxtail grass) is narrowly restricted to sandy soils at Pt. Reyes with *Deschampsia caespitosa* prairie.

A few sensitive wildlife species are known to depend on coastal prairie habitat. The endangered *Cicindela ohlone* (Ohlone tiger beetle) requires bare, disturbed areas within coastal prairie to feed and reproduce. It lives mainly in grazed and burned grasslands in Santa Cruz County. The muskrat-sized Pt. Arena mountain "beaver" *(Aplodontia rufa nigra)* is endemic to southern Mendocino County and coastal prairie

TABLE 7.7
Rough Classification of California Coastal Prairie Using Plot and Transect Data from Mendocino to San Luis Obispo Counties

	Type I: Annual Grassland		*Type II: Oatgrass*							*Type III: Moist Native Perennial Grassland*
			Subtype IIa		Subtype IIb			Subtype IIc		
	PLOT 1	PLOT 2	PLOT 3	PLOT 4	PLOT 5	PLOT 6	PLOT 7	PLOT 8	PLOT 9	PLOT 10
	Percent of Plots with Species Present									
Number of plots in the group	5	5	29	309	10	21	30	13	11	18
Characteristic Species										
*Bromus diandrus**	**100**	**100**	79	49	80	5	23	31	46	17
*Carduus pycnocephalus**	**80**	**60**	97	29	10	14	7	15	.	6
*Avena species**	**60**	**60**	35	22	10	5	.	46	.	.
*Hirschfeldia incana**	**100**	**20**	.	1	10	.	.	.	.	.
*Silybum marianum**	**60**	**40**	28	7	10	.	.	.	.	.
*Plantago lanceolata**	.	.	**55**	**90**	**100**	**86**	**67**	**85**	**82**	**72**
Danthonia californica	.	.	**17**	**91**	**100**	**95**	**40**	**100**	**64**	**44**
Ranunculus californicus	.	.	**3**	**40**	**80**	**57**	**80**	**15**	**55**	**28**
*Hypochaeris radicata**	.	.	**35**	**67**	**60**	**81**	**47**	**54**	**73**	.
Bromus carinatus	.	.	**48**	**31**	**80**	**100**	**57**	**62**	**18**	6
Nassella pulchra	.	40	**45**	**52**	**40**	**86**	**3**	**46**	.	6
Rubus ursinus	.	.	**14**	**16**	**80**	**48**	**47**	**69**	**55**	.
Sisyrinchium bellum	.	.	**3**	**59**	**90**	**81**	**43**	**77**	**55**	.
Achillea millefolium	.	.	**3**	**18**	**70**	**43**	**83**	**23**	**27**	.
Luzula comosa	.	.	.	**18**	**80**	**43**	**27**	**23**	**18**	.
*Aira caryophyllea**	.	.	.	**49**	**80**	**62**	**47**	**39**	**27**	.
Linum bienne	.	.	.	**56**	**10**	**76**	.	**62**	**46**	11
Juncus occidentalis	.	.	**3**	**32**	.	**33**	**3**	**15**	**55**	.
*Briza minor**	.	.	**14**	**56**	**20**	**71**	**20**	**46**	**36**	.
Eschscholzia californica	.	.	**28**	**13**	**50**	**5**	**17**	.	.	.
*Vulpia myuros**	.	.	**45**	**46**	**90**	**48**	**20**	.	.	11
*Sonchus oleraceus**	.	80	**38**	**12**	**20**	**38**	**17**	.	.	39
Juncus bufonius	.	.	**3**	**38**	**30**	**10**	**27**	.	36	11
*Trifolium dubium**	.	.	**17**	**58**	**10**	**19**	**7**	.	64	11
Baccharis pilularis	20	.	41	33	**60**	**86**	**80**	46	.	6
Deschampsia caespitosa	.	.	.	13	**60**	**76**	**80**	23	.	.
Iris douglasiana	.	.	.	12	**60**	**81**	**60**	31	.	.
Chlorogalum pomeridianum	.	.	14	25	**60**	**91**	**3**	.	.	.
*Holcus lanatus**	.	.	.	25	.	67	93	**100**	**100**	11
*Rumex acetosella**	.	.	10	58	50	29	93	**77**	**82**	50

(continued)

TABLE 7.7 (continued)

	Type I: Annual Grassland		*Type II: Oatgrass*							*Type III: Moist Native Perennial Grassland*
			Subtype IIa		Subtype IIb			Subtype IIc		
	PLOT 1	PLOT 2	PLOT 3	PLOT 4	PLOT 5	PLOT 6	PLOT 7	PLOT 8	PLOT 9	PLOT 10
	Percent of Plots with Species Present									
Characteristic Species										
*Poa pratensis**	.	.	.	4	.	.	67	**69**	**91**	11
*Danthonia pilosa**	.	.	.	5	.	24	3	**100**	**64**	.
Carex tumulicola	.	.	.	15	.	19	3	**77**	**46**	.
Juncus phaeocephalus	.	.	3	20	10	5	70	.	.	**100**
Hordeum brachyantherum	.	.	3	16	100	5	30	.	.	**94**
*Rumex crispus**	.	20	17	17	10	.	3	.	.	**83**
Carex species	.	.	3	10	20	14	47	.	9	**61**
*Lythrum hyssopifolia**	.	.	.	17	10	.	7	.	9	**56**
Oxalis albicans ssp. pilosa	.	.	3	17	10	14	23	8	.	**50**
Juncus patens	.	.	.	24	.	38	7	31	27	**50**
Other Species										
*Lolium species**	20	100	83	73	100	38	67	39	46	67
*Bromus hordeaceus**	20	20	72	78	70	67	10	54	73	22
*Anagallis arvensis**	.	60	41	76	80	57	40	39	18	78
*Geranium dissectum**	.	.	72	76	100	52	63	62	64	83
*Vulpia species**	.	100	55	52	10	38	17	62	55	33
*Sonchus asper**	.	.	45	24	10	48	30	46	.	83
*Trifolium subterraneum**	.	.	10	53	10	.	.	.	55	28
*Vicia species**	20	20	38	20	.	29	10	69	36	.
Pteridium aquilinum v. pubescens	.	.	.	11	10	14	3	39	27	.
Leymus triticoides	.	.	3	7	.	14	7	8	9	11
*Erodium moschatum**	.	100	7	9	60	.	.	.	9	6
*Hordeum murinum ssp. leporinum**	.	100	7	17	.	5	7	.	.	.
*Medicago polymorpha**	.	100	45	29	60	10	13	.	.	39

NOTE: From Hayes and Holl, 2003; Stromberg et al, 2002. Shown are 87 of the more than 490 documented species, grouped into 10 vegetation types, separated by Twinspan, with modification by Ayzik Solomeshch. Boldface cells help emphasize the three major different community types and that are discussed in the chapter. Community types: (I) California annual grassland; (II) California oatgrass; (IIa) typical subtype; (IIb) *Deschampsia cespitosa* subtype; (IIc) exotic perennial subtype; (III) moist native perennial grassland. Numbers in the body of the table are constancy (percent of plots with the species present); * indicates exotic species.

is among the habitats it occupies. Coastal populations of the American badger *(Taxidea taxus)* are fast disappearing due to habitat fragmentation. A large number of threatened butterfly species are associated with coastal prairie, including the myrtle silverspot (*Speyeria zerene* ssp. *myrtleae*—host plants: *Viola* spp.), Behren's silverspot (*S.z.* ssp. *behrensii*—host plant: *Viola adunca*), callippe silverspot (*S. callippe* ssp. *callippe*—host plants: *Viola* spp.), Palos Verdes blue *(Glaucopsyche lydamus* ssp. *palosverdensis*—host plants: *Lotus scoparius* and *Astragalus trichopodus var. lonchus)*, and Mission blue *(Plebejus*

TABLE 7.8
Plant Species Whose Populations Are Mainly Found in California's Coastal Prairie

Scientific Name	*Common Name*
Brodiaea terrestris	Dwarf Brodiaea
Brodiaea elegans	Elegant Brodiaea
Calandrinia ciliata	Red maids
Calochortus luteus	Yellow mariposa lily
Calochortus uniflorus	Large-flowered star tulip
Camissonia ovata	Sun cups
Carex brevicaulis	Short-stemmed sedge
Castilleja ambigua	Johnny nip
Castilleja densiflora var. *densiflora*	Purple owl's clover
Castilleja densiflora var. *noctuinus*	Night-scented owl's clover
Centunculus minimus	Chaffweed
Cicendia quadrangularis	Oregon timwort
Cirsium quercetorum	Brownie thistle
Clarkia davyi	Davy's Clarkia
Clarkia purpurea purpurea	Four spot
Chorizanthe robusta hartwegiana	Scotts Valley Spineflower
Danthonia californica	California oatgrass
Deschampsia caespitosa	Tufted hair grass
Dichondra donelliana	California ponyfoot
Dodecatheon clevelandii	Cleveland's shooting star
Hemizonia corymbosa	Coastal tarplant
Holocarpha macradenia	Santa Cruz sunflower
Horkelia marinensis	Pt. Reyes Horkelia
Juncus bufonius	Toad rush
Juncus occidentalis	Western rush
Lasthenia minor	Coastal goldfields
Lotus formosissimus	Coast trefoil
Microseris bigelovii	Coast Microseris
Microseris paludosa	Swamp dandelion
Perideridia gairdneri	Gairdner's Yampah
Plagiobothrys chorisianus	Artist's popcornflower
Plagiobothrys diffusus	San Francisco popcornflower
Sanicula arctopoides	Footsteps of spring
Scirpus cernuus	Annual Scirpus
Scirpus koiolepis	Keeled bulrush
Sidalcea malvaeflora	Checkerbloom
Spiranthes romanzoffiana	Western ladies tresses
Trifolium buckwestiorum	Santa Cruz clover
Trifolium variegatum,	Many other clovers
T. barbigerum,	
T. microdon,	
T. depauperatum,	
T. appendiculatum, T. grayi,	
T. truncatum	
Triphysaria eriantha ssp. rosea	Pink butter 'n eggs
Triphysaria versicolor ssp. faucibarbata	Yellow owl's clover
Triphysaria versicolor ssp. versicolor	Yellow owl's clover
Triteleia hyacinthina	Hyacinth flowered Brodiaea
Zigadenus micranthus var. fontanus	Fountain death-camas
Zigadenus fremontii var. minor	Dwarf star lily

NOTE: Sensitive species are separately listed in Table 7.9.

icarioides ssp. *missionensis*—host plants: perennial *Lupinus* spp.*)* butterflies, as well as Opler's long-horned moth (*Adella oplerella*—host plant: *Platystemon californicus*). A number of sensitive amphibians are associated with coastal prairie, including the San Francisco garter snake (*Thamnophis sirtalis* ssp. *tetrataenia* and the California red-legged frog (*Rana draytonii*).

CONSERVATION AND RESTORATION ISSUES

It has been common practice to assess the conservation value of sites containing coastal prairie by recording a visual estimate of the percentage cover of *Danthonia californica*, *Nassella pulchra*, *Festuca idahoensis*, and *Deschampsia caespitosa*, indicator species for coastal prairie (Munz and Keck

TABLE 7.9
Sensitive Plant Species of California Coastal Prairie

Scientific Name	*Family*	*Occurrence*[a]	*CNPS*[b]	*State*[c]	*Federal*[d]
Astragalus tener var. *titi*	Fabaceae	Coastal bluff scrub, coastal prairie, GV, CCo, SnFrB	1B	CE	FE
Blennosperma nanum var. robustum	Asteraceae	Coastal prairie, coastal scrub, NCo	1B	n/a	n/a
Campanula californica	Campanulaceae	Bogs and fens, closed-cone coniferous forest, coastal prairie, meadows and seeps, marshes and swamps (freshwater), north coast coniferous forest, NCo, CCo	1B	n/a	n/a
Chorizanthe cuspidata var. cuspidata	Polygonaceae	Coastal bluff scrub, coastal dunes, coastal prairie, coastal scrub, SnFrB, NCo	1B	n/a	n/a
Chorizanthe cuspidata var. villosa	Polygonaceae	Coastal dunes, coastal prairie, coastal scrub, NCo	1B	n/a	n/a
Chorizanthe howellii	Polygonaceae	Coastal dunes, coastal prairie, coastal scrub, NCo	1B	CT	FE
Chorizanthe robusta var. hartwegii	Polygonaceae	Meadows and seeps, valley and foothill grassland, coastal prairie, CCo	1B	n/a	FE
Chorizanthe valida	Polygonaceae	Coastal prairie, NCo	1B	CE	FE
Cirsium occidentale var. *compactum*	Asteraceae	Coastal scrub and coastal prairie, CCo	1B	n/a	n/a
Clarkia franciscana	Onagraceae	Coastal scrub, valley grassland, serpentine, SnFrB	1B	CE	FE
Deinandra increscens ssp. *villosa*	Asteraceae	Coastal bluff scrub, coastal scrub, valley grassland, s CCo	1B	CE	FE
Delphinium luteum	Ranuculaceae	Coastal scrub, coastal prairie, moist cliffs, n CCo	1B	CR	FE
Eriogonum luteolum var. caninum	Polygonaceae	Chaparral, coastal prairie, valley and foothill grassland, NCo	3	n/a	n/a
Hemizonia congesta ssp. tracyi	Asteraceae	Coastal prairie, lower montane coniferous forest, north coast coniferous forest, NCo	4	n/a	n/a
Centromadia parryi ssp. congdonii	Asteraceae	Valley and foothill grassland, coastal prairie, SnFrB, CCo	1B	n/a	n/a
Holocarpha macradenia	Asteraceae	Coastal prairie, coastal scrub, valley and foothill grassland, NCo, SnFrB, CCo	1B	CE	FT
Lilium occidentale	Liliaceae	Coastal bluff scrub, coastal scrub, coastal prairie, n NCo, sw OR	1B	CE	FE
Limnanthes douglasii ssp. sulphurea	Limnanthaceae	Coastal prairie, meadows and seeps, marshes and swamps (freshwater), vernal pools, NCo, CCo	1B	CE	n/a

TABLE 7.9 (continued)

Scientific Name	*Family*	*Occurrence*[a]	*CNPS*[b]	*State*[c]	*Federal*[d]
Limnanthes vinculans	Limnanthaceae	Coastal prairie, meadows and seeps, valley and foothill grassland, vernal pools, NCo	1B	CE	FE
Leptosiphon acicularis	Polemoniaceae	Chaparral, cismontane woodland, coastal prairie, valley and foothill grassland, NCo, CCo, SnFrB	4	n/a	n/a
Linanthus grandiflorus	Polemoniaceae	Coastal bluff scrub, closed-cone coniferous forest, cismontane woodland, coastal dunes, coastal prairie, coastal scrub, valley and foothill grassland, NCo, CCo, SnFrB, TR	4	n/a	n/a
Micropus amphibolus	Asteraceae	Broadleafed upland forest, chaparral, cismontane woodland, valley and foothill grassland, coastal prairie, NCo, SnFrB, CCo, TR	3	n/a	n/a
Microseries paludosa	Asteraceae	Coastal prairie, closed cone pine forest, cismontane woodland, coastal scrub, valley and foothill grassland, CCo, SnFrB	1B	n/a	n/a
Plagiobothrys chorisianus	Boraginaceae	Chaparral, coastal prairie, coastal scrub, closed cone pine forest, vernal pools, marshes and swamps, SnFrB, CCo	1B	n/a	n/a
Plagiobothrys diffusus	Boraginaceaae	Coastal prairie, valley and foothill grassland, SnFrB, CCo	1B	CE	n/a
Polygonum hickmanii	Polygonaceae	Coastal prairie, valley and foothill grassland, CCo	1B	CE	FE
Potentilla hickmanii	Rosaceae	Coastal bluff scrub, vernally wet meadows, CCo, NCo	1B	CE	FE
Sanicula maritima	Apiaceae	Coastal prairie, valley grassland, wet meadows and ravines, CCo, SnFrB	1B	CR	n/a
Stebbinsoseris decipiens	Asteraceae	Chaparral, coastal prairie, meadows and seeps, Valley and foothill grassland, SnFrB, CCo	1B	CR	n/a
Trifolium amoenum	Fabaceae	Coastal prairie, valley and foothill grassland, coastal bluff scrub, NCo, SnFrB, CCo	1B	n/a	FE
Trifolium grayii	Fabaceae	Coastal prairie, NCo, CCo	n/a	n/a	n/a
Trifolium buckwestiorum	Fabaceae	Broadleafed upland forest, cismontane woodland, coastal prairie, NCo, CCo	1B	n/a	n/a
Trifolium polyodon	Fabaceae	Coastal prairie, closed cone coniferous forest, meadows and seeps, valley and foothill grassland, CCo	1B	CR	n/a
Triphysaria floribunda	Schrophulariaceae	Valley and foothill grassland, coastal prairie, coastal scrub, NCo	1B	n/a	n/a

[a]Occurrence (CNPS 2005; Hickman 1993): CCo = Central Coast; ChI = Channel Islands; GV = Great Central Valley; NCo = North Coast; NCoRO = Outer North Coast Ranges; OR = Oregon; SnFrB = San Francisco Bay

[b]CNPS Codes: 1B = Rare, threatened, or endangered in California and elsewhere

[c]State Codes: CE = California endangered; CT = California threatened; CR = California rare

[d]Federal Codes: FE = Federal Endangered; FT = Federal Threatened

1959). However, there is no agreed-on threshold value for percentage of cover of native grasses to delineate coastal prairie (Todd Keeler-Wolf personal communication). Data collected in the spring from numerous locations throughout the geographic extent of remaining coastal prairie areas suggest that few areas contain >15% relative cover of all native perennial grasses (Hayes, unpublished data). As there are no precontact data on the cover or extent of native grasses, it is difficult to assess or predict the potential cover for restoration purposes.

There is, however, sufficient literature about the perennial native grasses to reach a few important conclusions:

1. Even in relatively intact areas, there have been historic factors such as overgrazing, disease, drought, and competition with exotic, invasive species (in combination or alone) that have caused native perennial grasses to decline (Barry 1972; Painter 1995).
2. Perennial grasses experience extreme competition with exotic species, especially exotic annual grasses (Bartolome et al. 1986).
3. Apart from competition, the establishment and growth of nature perennial grasses are limited primarily by edaphic factors in xeric areas and by seed dispersal in mesic areas (Dyer, Fossum et al. 1996; Seabloom et al. 2002).
4. Perennial grasses, like most grassland species, are patchily distributed through any given grassland.

It is evident that the delineation of coastal prairie should be informed by the presence, even in low numbers and in diffuse patches, of perennial bunchgrasses. There is no known correlation between biotic values of dense versus diffuse stands of native perennial grasses. The absence of native perennial grasses at one moment in time may not mean that there has been local extinction, because native propagules may still exist in the seed bank. There are two types of grasslands that have little potential to contain an intact assemblage of native plants, hence have low potential for restoration. First, there are areas degraded by prior agriculture ("old fields")? Once an area has been intensely cultivated, irrigated, or fertilized, there is only a slight chance that it maintains an intact native plant community, even in the soil seed bank. In such cases, there will be no native grasses in the center of the field, as dispersal will be very slow and only along the border (Stromberg and Griffin 1996).

The second type of grassland with little potential for native plant diversity and restoration is one that has been type converted from some other vegetation. It was historically common for ranchers to convert oak and scrub habitat to open grassland, and these areas may have yet to acquire little of the plant species diversity typical of climax grassland (Huenneke and Mooney 1989).

If grassland does not meet the above two criteria, then it may be useful to make an intensive survey. The first stage of assessment should be a thorough documentation of the density and distribution of native perennial grasses. Mapping patches where their density is high may help identify historic land-use boundaries.

Coastal prairie is considered a sensitive plant community by the California Department of Fish and Game and the California Coastal Commission. Several counties have therefore taken steps to protect the habitat through ordinances. These legal protections have led to various restoration projects. Often, the mitigation for "taking" areas of coastal prairie for development includes the planting of native grasses in areas of degraded grasslands, and then managing and monitoring these areas for a short period of time. No projects have succeeded to date in establishing self-sustaining populations of native grasses or replicating the species richness of more intact coastal prairie.

Management of existing prairie areas to enhance and maintain native species has been somewhat more successful. Early studies raised concerns about the loss of coastal prairie to northern coastal scrub invasion after the removal of grazing (McBride 1974). All but the bald hills (introduced annuals) form of coastal prairie appears to be vulnerable to invasion of scrub. A complete transformation of grassland to scrub can occur in 15 to 25 years. Fire seems largely incapable of halting brush invasion, because many scrub species resprout, germinate, or in other ways are fire tolerant. Coastal prairie areas adjacent to pine and Douglas-fir populations are vulnerable to tree invasion, as well. Experiments are now taking place at Salt Point State Park in mechanical removal of invading pines in order to enhance the grasslands.

Anecdotal evidence suggests that mowing and focused weed removal increase native species richness and cover by stimulating recovery of the native seedbank at one site in southern Santa Cruz County (Dremann and Shaw 2002). Another study, in San Mateo County, examined the efficacy of fire alone or in conjunction with grazing, and concluded that California oatgrass responded positively to grazing but other species had less predictable responses to management (Hatch, Bartolome et al. 1999). A study examining coastal prairie plant guild responses to grazing or cessation of grazing suggests that grazing may enhance the species richness and cover of native annual forbs in comparison with areas where grazing no longer occurs, whereas native grasses are unaffected (Hayes and Holl 2003).

A few attempts have been made in the use of biological control to reduce the abundance of particularly noxious weed species in coastal prairie. The most successful was the introduction of Klamath weed beetle *(Chrysolina quadrigemina)* in 1946 to control *Hypericum perforatum*. Introduced around the turn of the century, *Hypericum perforatum* had spread to completely dominate about 1 million ha of coastal prairie by 1945. Its abundance had negative economic consequences for cattle owners: the invasive plant caused exposed skin (not covered with hide) to become blistered and sensitive, leading to decreased foraging and slower growth of the animals. Within 2 years of the insect's release, grassland cover by *H. perforatum* decreased from 58% to

>1%, and at the same time the cover of native bunchgrasses, such as Danthonia californica, rose from 9% to 23%. Ten years after the insect's release, bunchgrass cover had risen to 45% (Huffaker and Kennett 1959).

Areas for Future Research

Future research related to management of northern coastal scrub should address the following important questions:

1. What are the correct classifications of the multiple series and associations that contribute to coastal bluff scrub?
2. What factors facilitate the predominance of California sagebrush and the reduction of coyote brush at the inland margins of coastal scrub?
3. What are the extents and locations of the various series of northern coastal scrub and of the different succession seres of those scrublands; describe their relative potentials as fire hazard and special-status species habitat; describe the succession seres to conifers, and likelihood of such succession near the coast and in the north; determine the effects of long-term absence of disturbance and the locations of the oldest scrub stands.
4. What are appropriate and feasible management targets and models of the landscape mosaics of northern coastal scrub and coastal prairie in dynamic interaction? How do we design appropriate disturbance regimes, including prescribed burning, livestock grazing, and surrogates to manage for that mosaic?

The greatest threats to the continued health of remaining areas of coastal prairie include development pressure, lack of appropriate disturbance regimes, and weed invasion. Future research could address the following important questions:

1. How do we determine the ecological value of any coastal grassland?
2. Is there a feasible way to determine the potential to restore a site to coastal prairie, from an existing seedbank?
3. How do we design appropriate disturbance regimes to manage for a suite of species with conflicting responses to disturbance, on the landscape level?
4. If we cannot control their invasion, how do we best ameliorate the effects of invading nonnative perennial grasses?
5. How do we use fire as a viable management tool in coastal prairie?

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