Vegetation of Santa Cruz and Santa Catalina Islands

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INTRODUCTION

Most research on the plant geography of the Southern California Channel Islands has focused on the flora, perhaps inspired most by the large number of endemic species found there. The question of insular geographic isolation has led to evaluation of the island flora from several standpoints, including: interisland and island-mainland species affinities; island size, habitat diversity, and species richness; and the general question of island endemism, autochthonous evolution, and the islands as refugia for species having former widespread distributions on the continent (Philbrick 1967).

However, overall, the vegetation of the Channel Islands is not well known. No vegetation maps have ever been produced, as these areas have escaped previous statewide vegetation surveys, including the Vegetation Type Map Survey and the State Cooperative Soil-Vegetation Survey (Colwell 1977). Small-scale renditions shown as part of larger maps are lacking in detail and contain significant errors (U.S. Dept. Agric. 1945, Kuchler 1977). Broad plant communities are generally recognized, but actual distributions have been only informally discussed (Raven 1963, Thorne 1967, Philbrick and Haller 1977). As an initial attempt at describing the plant cover of the Channel Islands, this study presents vegetation maps of Santa Cruz and Santa Catalina Islands as interpreted from color infrared aerial photography. The maps are drafted in color on eight 1:24,000 scale (7½ minute) U.S. Geological Survey topographic quadrangles (four for each island), and reduced to the format of this volume. The vegetation maps offer just one "snapshot" of a "motion picture" which shows plants in constant change. The vegetation is dynamic; changes are especially rapid in areas where feral herbivores are being controlled. The discussion to follow describes plant community distributions, physiognomic characteristics, and species dominance.

THE PHYSICAL ENVIRONMENT

Santa Cruz and Santa Catalina Islands are among the largest and most diverse of the Channel Island group, having respective areas of 249 and 194 km^2. Approximately 30 km in length, both islands are roughly east-west in orientation and consist of moderately dissected parallel ridges reaching 400 to 700 m elevation. Except in valley bottoms and ridgelines, most slopes are steeper than 20 degrees, but less than 30 degrees.

The climate is Mediterranean with mild temperatures, rainy winters, and dry summers. Winter precipitation results chiefly from frontal disturbances guided into southern California from the north Pacific Ocean by troughs (waves) in upper-level westerly circulation between November and April. The annual precipitation on Santa Catalina ranges from 200 mm at Little Harbor on the southwest to 350 mm on the channel slope in the vicinity of Avalon. Because of Santa Cruz Island's greater size and orographic influences of the Santa Ynez Mountains to the north, the annual precipitation is much greater. The Stanton Ranch in the interior central valley of Santa Cruz averages nearly 500 mm (data on file at the Stanton Ranch) with higher slopes to the west receiving perhaps as much as 600 mm. The predominance of large-scale air masses associated with the polar front jet stream minimizes island-mainland climatic differences during this season.

During summer, dynamic subsidence, associated with the surface Pacific high pressure system and weak anticyclonic circulation aloft, is dominant as cyclonic storms travel far to the north of southern California. Although the regional air mass is warm and dry, surface weather on the Channel Islands is strongly influenced by a shallow, coastal marine layer (a cool, moist, low-level air mass 300 to 800 m in vertical depth) which advects slowly south and eastward toward interior California from the cold, upwelling Pacific Ocean waters along the coast. It is the day-to-day persistence of the marine layer that ameliorates and differentiates island climate from that of the mainland during the summer drought season. Because Santa Cruz Island is located in exposed outer channel waters, annual temperatures there, especially in coastal areas facing west and north, are probably a few degrees colder than at Santa Catalina, which is sheltered in the southern California embayment. Diabatic heating and turbulent mixing of the marine layer with warmer air above rough terrain still produce noticeably warmer temperatures in the interior portions of both islands, particularly in the central valley of Santa Cruz Island (Hochberg 1980) where daytime temperatures are not unlike those in mainland coastal mountains and valleys as far inland as 20 km.

The islands have been overgrazed by feral goats, sheep, pigs, and other introduced domestic animals for more than a century. Historical records indicate that grazing, mostly by sheep, became important soon after statehood (1850) at a time when these activities were widespread in the coastal plains and mountains of southern California (Brumbaugh 1980, Coblentz 1980, Minnich 1978). The goat may have been introduced to Santa Catalina during the late Mexican period (Coblentz 1980). These animals gradually became feral and multiplied at will in the absence of indigenous predatory animals. Herds increased rapidly to tens of thousands and had so much impact on the vegetation that Santa Cruz Island was "ravaged" by the time of the 100th meridian survey of 1875 (Rothrock, in Wheeler 1876); ground photographs of Santa Catalina taken in the 1880s show strong evidence of vegetation stripping at present-day Avalon, the isthmus, and other sites (Huntington Library Photo Collection). Some measures have been taken to control these animals in the present century. Under the ownership of the Stanton family, portions of Santa Cruz Island—notably on the isthmus, in Central Valley, in several western drainages, and more recently in the southern drainages—have been fenced to keep sheep out. On Santa Catalina, commercial sheep and cattle grazing continued until the early 1950s when domestic stock were successfully removed (A. Douglas Probst, pers. comm.). Goats were also recently exclosed from interior drainages east of the Middle Ranch on Santa Catalina. Although goats are free to roam over major portions of the Island, the intensity of grazing pressure seems to be partly determined by behavior and territoriality of the animals (Coblentz 1976). Severest grazing appears to occur in Silver Canyon, Grand Canyon, the channel slope in the vicinity of Twin Rocks, and west of the isthmus. Herds on both islands are intermittently reduced by hunting.

METHODS

The vegetation maps were interpreted from 1:22,000 scale color infrared (CIR) photography (type 2443) done in July, 1970 (Santa Cruz Island) and February, 1976 (Santa Catalina Island). The film was reproduced on nine-inch square positive transparencies and properly exposed, except for some vignetting. (Color imbalance of the Santa Catalina photography was compensated for by excellent resolution.)

The photography was interpreted over a light table with a Bausch and Lomb rollfilm stereoscope with 3.3x and 8.8x magnification. There was no field mapping; rather, the primary role of fieldwork was the characterization of photographic data. The physiognomic vegetation classes were easily identified on the basis of crown structure, height, spread, and other morphological characteristics. In taxonomic identification from aerial photographs, on the other hand, the imagery appearance of a species had to be as familiar as its field appearance.

This involved conventional taxonomic identification in the field and determination of gross physical features which made plant species recognizable at a distance and ultimately from above. The process was one of cross-checking information from the field and from photographs. In the field, individual plants were located and plotted on topographic quadrangles and checked against photographs of the same area. In the laboratory, plant signatures on photography were extrapolated to other areas and checked in the field in order to develop consistent species identification. Species were identified singly or narrowed down into species "sets," often to the genus level (*e.g.*, *Arctostaphylos*) or physiognomic class (*e.g.*, coastal sage scrub, grassland). Instead of using an *a priori* typing system, the plant classification is based on information which could be interpreted from the photography.

The vegetation maps are both floristic and physiognomic constructs for which the data are shown by linework and color, respectively. Linework delimits polygons of individual species or species sets defined by a minimum cover threshold of 20 per cent. Polygons may overlap where species are found together. In areas of chaparral, color and linework may operate independently; here, colorwork denotes the dominant physiognomic layer defined in terms of equal abundance of individual physiognomic classes as observed from above in aerial photographs. Thus, a polygon deliminating an open stand of scrub oak (*Quercus dumosa*) underlain by contiguous grass is ascribed the color for grassland vegetation. Conversely, a contiguous cover of *Quercus dumosa* underlain by open grass is given the color for chaparral. Similarly, if the point of equal abundance of *Quercus dumosa* and grass falls within the polygon, a color boundary dividing both physiognomic classes may transect the polygon. For other vegetation types, the species mapped and colorwork for physiognomy are conformal. Areal data for the vegetation types were computed by areagram overlay on the maps (3 per cent error) and are shown in Tables 1 to 4. The author concedes that there may be errors in the maps because the detail of information gained from the air cannot match that which can be seen on the ground. The aerial view, on the other hand, allows for more efficient mapping of large areas by providing greater overall perspective of the spatial relations among plants, and will be useful until detailed field-mapping is done.

PRESENT VEGETATION

At the physiognomic level, the prevailing plant communities of Santa Cruz and Santa Catalina Islands are comparable to those found on mainland coast ranges. They include annual grassland, coastal sage scrub, chaparral, oak woodland, riparian woodland, and closed-cone pine forest. Cursory examination of the vegetation maps (Figs. 1 and 2) shows that the distribution of shrub and woodland vegetation is highly fragmented, covering mostly canyons and north-facing slopes, except at the east end of Santa Catalina where cover is continuous. Herbaceous vegetation prevails elsewhere. For the most part, the same species form the bulk of vegetal cover of both islands; some differences in the geographic patterning are evident, however, which seem to reflect important contrasts in their respective climates and grazing histories.

Grassland

Annual grasses form the major portion of the total vegetal cover of both islands. Field reconnaissance indicates that the dominant species are introduced European grasses, such as *Avena fatua*, *A. barbata*, *Bromus rigidus*, and *B. rubens*, although local depauperate populations of native perennial grasses, *e.g.*, *Stipa pulchra*, may be found. Annual grassland seems to thrive best in deep loamy soils on alluvium or marine terraces, particularly in Central Valley, at the isthmus ridge, and on the west side of Santa Cruz Island. However, grassland may even prevail on steep rocky slopes, though usually admixed with woody vegetation. Herbaceous cover is completely absent only in relatively undisturbed coastal sage scrub and chaparral, such

TABLE 1. Vegetation summary of Santa Catalina and Santa Cruz Islands: physiognomic types (hundreds of hectares).

Physiognomic type[1]	S. Catalina	S. Cruz
n	194.0	249.0
Grassland	59.0	114.6
Coastal sage scrub	25.3	14.1
Prickly pear (*Opuntia*)	13.0	7.7
Chaparral	81.1	76.2
Oak woodland	2.6	17.5
Conifer forest	0.0	5.3
Riparian	0.3	2.6
Cultivated	3.1	0.6
Urban	1.4	0.0
Bare	8.2	10.4

[1]Area defined by dominant vegetal layer.

TABLE 2. Vegetation summary of Santa Catalina and Santa Cruz Islands: woodland, riparian, and sage species (hundreds of hectares).

Woodland, riparian, and sage species[1]	S. Catalina	S. Cruz
Lyonothamnus floribundus	0.3	3.0
Prunus lyonii	2.0	2.6
Quercus agrifolia	0.0	11.4
Q. chrysolepis	0.1	0.4
Q. tomentella	0.2	0.1
Pinus muricata	0.0	5.3
Baccharis glutinosa	—[2]	1.4
B. pilularis	0.2	4.0
Populus fremontii	0.2	0.4
Salix spp.	0.1	0.8
Artemisia, Salvia, spp.	38.8	15.3
Opuntia littoralis	15.0	9.1
Annual grasses	100.4	160.0

[1]Includes stands sympatric with chaparral.
[2]Present, but in insignificant amounts.

TABLE 3. Vegetation summary of Santa Catalina Island: chaparral (hundreds of hectares).[1]

Vegetation type	Contiguous stands	Sympatry with: Sage	Grass	Opuntia	Total	Per cent contiguous
Adenostoma fasciculatum	0.6	0.4	0.9	—[2]	1.9	32
Arctostaphylos catalinae	—[2]	0.0	0.0	0.0	—[2]	—[2]
Heteromeles arbutifolia	14.0	0.8	17.0	0.2	32.0	44
Malosma (Rhus) laurina	1.1	1.3	2.4	1.2	6.0	18
Mixed (*Ceanothus megacarpus, C. arboreus, Cercocarpus betuloides*)	3.8	0.3	0.4	0.0	4.5	84
Quercus dumosa	24.0	1.2	23.4	0.2	48.8	49
Rhus integrifolia	3.3	10.8	14.7	0.6	29.4	11

[1]Area defined by 20 per cent cover and will overlap other types (values are not additive). [2]Present, but in insignificant amounts.

TABLE 4. Vegetation summary of Santa Cruz Island: chaparral (hundreds of hectares).[1]

Vegetation type	Contiguous stands	Sympatry with: Sage	Grass	Opuntia	Total	Per cent contiguous
Adenostoma fasciculatum	0.6	0.3	1.7	0.0	2.6	23
Arctostaphylos spp.	6.2	—[2]	2.3	—[2]	8.5	73
Mixed (*Ceanothus megacarpus, C arboreus, Cercocarpus betuloides*)	0.1	0.4	3.8	—[2]	4.3	2
Quercus dumosa (Heteromeles arbutifolia)	16.3	2.2	33.8	1.0	54.3	30
Rhus integrifolia	—[2]	2.3	3.8	0.4	6.5	—[2]
Totals	23.2	5.2	45.4	1.4	76.2	30

[1]Area defined by dominance. [2]Present, but in insignificant amounts.

as at the Avalon end of Santa Catalina.

The density and cover of annual grassland varies significantly depending on grazing history. On Santa Cruz Island, grass quality is closely related to fencing history and sheep grazing (Orme and Minnich 1970). Grass is tall (*ca.* 1.0 m) and contiguous in areas free of sheep. Moderate grass cover occurs along the southern drainages where sheep have been managed since the 1950s. Cover is sparse in areas of heaviest sheep concentration, particularly the Devils Peak ridge north of Central Valley and "No Man's Land" southeast of Chinese Harbor. Grass quality on Santa Catalina Island also ranges from excellent to very poor, but occurs in a gradient having little correlation with fencing, perhaps owing to the territorial behavior of goats (Coblentz 1976). Poorest grass cover occurs where goat populations are highest (Silver Canyon, the channel slope near Twin Rocks, and west of the isthmus). Grass cover is best along the channel slope between Mt. Black Jack and Swains Canyon, and within the Wrigley and Middle Ranches.

Grass cover also varies seasonally. Germination and early growth occurs during winter and spring throughout the islands except in the most severely eroded areas. Normally, grasses keep up with grazing pressure until drought desiccation begins in late spring or early summer. By autumn, most herbaceous cover accessible to feral animals is stripped, except for toxic species such as *Eremocarpus setigerus* and *Mimulus longiflorus*.

Coastal Sage Scrub

Coastal sage scrub occurs primarily on south-facing slopes on over 20 per cent of Santa Catalina Island and over only 6 per cent of Santa Cruz Island. On Santa Cruz, coastal sage scrub is restricted to areas free of sheep. Largest stands occur where prevailing grass quality is best: on the south face of the isthmus, in Central Valley, and on the southwest end from Cañada Posa to Morse Point (also near Bowen Point). On Santa Catalina, the vitality of coastal sage scrub is inversely related to the intensity of goat grazing. Contiguous stands reminiscent of coastal sage scrub on nearby mainland mountain ranges (0.5 to 1.0 m tall; greater than 70 per cent cover) are widespread at the east end in the vicinity of Avalon. These contiguous stands grade into fragmented, degraded stands infested with prickly pear (*Opuntia*) toward the west into the interior drainages of the Wrigley and Middle Ranches and into the isthmus area. Field observations indicate the dominant species are *Artemisia californica, Salvia apiana*, and a procumbant *S. mellifera*.

Two evergreen sclerophyll shrubs, *Rhus integrifolia* and *Malosma (Rhus) laurina*, are also sympatric with coastal sage scrub over extensive areas of Santa Catalina and locally on Santa Cruz Island. *Baccharis pilularis* ssp. *consanguinea* appears to be invading annual grassland on protected southern and western portions of Santa Cruz Island. In areas where goats are most concentrated on Santa Catalina, *Opuntia* is dominant, although isolated individuals of coastal sage species may be found amidst dense *Opuntia* thickets. *Opuntia* on Santa Cruz Island is in poor condition, due to the introduction of the cochineal bug in the 1930s, and normally does not harbor browse-sensitive plants.

Endemic species of *Eriogonum* appear to be less resilient to grazing than the dominant shrubs. *Eriogonum grande* and *E. arborescens* occur only in local populations in the best protected areas on Santa Cruz. *E. giganteum* on Santa Catalina is most conspicuous around Avalon and the Wrigley Ranch. *Artemesia californica* is also subject to browsing, and it, too, is most abundant near Avalon and the Wrigley Ranch.

Chaparral

In large part, island chaparral is dominated by species familiar on the mainland. Yet the physiognomy of this association differs in terms of stand maturity, openness of cover, and

diversity of growth form, ranging from tall "elfin forests" (sometimes grading into woodlands) to prostrate mats in wind-exposed locations on the north- and west-facing coasts. Chaparral rarely forms extensive cover except on north-facing slopes and canyons. The largest continuous stands on Santa Catalina Island occur on the channel slope between Swains Canyon and Avalon. On Santa Cruz Island the largest stands are along the north slope of Central Valley. Only one third of the stands have continuous cover. The remainder exist in parklands of primarily tall shrubs with sharp browse lines, underlain by annual grassland, coastal sage scrub, or prickly pear.

Broad floristic trends are common to both islands. The sumacs—*Rhus integrifolia* and *Malosma (Rhus) laurina* (Santa Catalina only)—tend to form open stands on south-facing slopes with an understory matrix of coastal sage scrub in protected areas, and grassland or prickly pear in overgrazed areas. *Malosma laurina* is most abundant in warmer interior portions of Santa Catalina. *Rhus integrifolia* is also almost ubiquitous over the island. On Santa Cruz, *R. integrifolia* is generally restricted to coastal localities.

On north-facing slopes, chaparral is dominated primarily by *Quercus dumosa*. *Rhus integrifolia* often forms an understory to the oak, especially on Santa Catalina. *Heteromeles arbutifolia* is locally dominant at coastal locations and in many mesic canyon sites elsewhere. *Cercocarpus betuloides* and *Ceanothus arboreus* are sparingly present in heaviest stands but normally absent from chaparral savannas. *Arctostaphylos* chaparral (*A. subcordata, A. insularis, A. tomentosa*) covers several areas of Santa Cruz Island, mostly gentle slopes and ridgelines south of the rift valley and along the crest of the isthmus. *Arctostaphylos* chaparral on Santa Catalina (*A. catalinae*) consists of only five unmappable populations amounting to a few hectares (Thorne 1967). Surprisingly, chamise chaparral (*Adenostoma fasciculatum*), widespread in southern California coastal mountains, is scarce on both islands. *Adenostoma* normally appears as a minor element of *Quercus dumosa* or *Arctostaphylos* chaparral. It is locally dominant, however, on mostly southern exposures; the most extensive stand (approximately 50 hectares) occurs just west of the Santa Catalina isthmus (a northern exposure). Open stands, widely admixed with *Ceanothus megacarpus* var. *insularis, Cercocarpus betuloides*, and *Quercus dumosa*, cover xeric slopes immediately north of the central rift valley of Santa Cruz Island. These also contain rare populations of *Rhus ovata* and *Rhamnus crocea* var. *pirifolia*. A prostrate ecotype of *Adenostoma fasciculatum* is also found at several locations on the island (*e.g.*, the isthmus and the ridgeline south of Cañada Cervada; Philbrick and Haller 1977).

Examination of the vegetation map shows that the floristic composition of Santa Cruz Island chaparral appears to be quite responsive to large climatic contrasts between the coast and the warmer, interior Central Valley. *Quercus dumosa, Heteromeles arbutifolia*, and *Rhus integrifolia* appear to be the only shrubs tolerant of the cold summers at the west end. In contrast, *Arctostaphylos, Adenostoma, Ceanothus megacarpus*, and *Cercocarpus* chaparral tend to be concentrated on interior sites.

The species richness of Santa Catalina Island chaparral appears to be inversely related to grazing pressure. In least disturbed areas around Avalon and the Middle and Wrigley Ranches, *Quercus dumosa* and *Heteromeles arbutifolia* are admixed with *Cercocarpus betuloides, Ceanothus arboreus*, and *C. megacarpus*, with embedded patches or understory of *Adenostoma fasciculatum* and coastal sage scrub on drier sites. Stands are mostly contiguous, have minimal browse damage, contain abundant fuels and, in the vicinity of Avalon, provide enough of a fire hazard to induce the Los Angeles County Fire Department to construct fuel breaks along ridgelines. In areas of heavier grazing, chaparral is dominated by the most durable robust shrubs, notably *Quercus dumosa* and *Heteromeles arbutifolia*. Stands are open, exhibit browse lines, and contain more herbaceous understory. *Malosma laurina* and *Rhus integrifolia*, however, seem to persist in the most goat-infested parts of Santa Catalina Island. In fact, the absence of browse lines on *Malosma laurina* in Grand Canyon suggests this species is somewhat protected by being unpalatable. On Santa Cruz, browse sensitive *Adenostoma* and *Ceanothus* species are also most abundant within areas protected from sheep, especially in Central Valley. A large stand of huge *Cercocarpus betuloides* (>6 m tall) occurs on south-facing slopes of the heavily grazed east end of Devils Peak ridge.

Many other chaparral species occur on the islands but are not abundant enough to be mapped. These include *Xylococcus bicolor, Garrya* spp., *Toxicodendron diversilobum, Comarostaphylis diversifolia, Rhamnus crocea* var. *pirifolia*, and the island endemic, *Crossosoma californicum*.

Oak Woodland

Mesic north-facing slopes, canyons, and bottomland support medium- to large-spreading trees, mostly of the genus *Quercus*, grouped in contiguous woodlands. The areal extent of this physiognomic type is more localized than chaparral, with the majority of populations occurring on Santa Cruz Island. On Santa Catalina, woodlands are narrowly confined to watercourse environments. The distribution of woodlands appears to be independent of grazing pressures because many of the best stands occur in areas heavily populated with sheep and goats.

Most woodlands on Santa Cruz consist of *Quercus agrifolia*, which is distributed along watercourses throughout the island. The most impressive stands occur in upper Cañada Cervada, in the interior Central Valley, and in the gorge draining Central Valley to Prisoners Harbor. Along the western channel slope of the heavily grazed Devils Peak ridge, *Quercus agrifolia* forms an extensive open parkland savanna covering ridges as well as canyons. Strangely, *Quercus agrifolia* is absent from Santa Catalina Island. Instead, the dominant woodland species here is *Prunus ilicifolia lyonii*, which occurs mostly along dry canyon bottoms. The finest populations are found at Cherry Cove west of the isthmus. On wetter Santa Cruz, *Prunus ilicifolia lyonii* mimics *Quercus agrifolia* by straying away from watercourses to cover rocky slopes and ridges, but rarely forms continuous cover as on Santa Catalina.

The islands share three additional oaks with localized distributions. Two species, *Q. chrysolepis* and *Q. tomentella*, form a hybrid complex in which expressions of each are found in divergent habitats. Small *Q. chrysolepis* patches cover the highest ridges of both islands (Santa Cruz: north slope of Devils Peak ridge; Santa Catalina: Mt. Orizaba, lower Cape Canyon). *Q. tomentella* occurs in cool, coastal localities, but often as solitary trees. The most impressive stands are found on Santa Catalina in Gallagher Canyon (Thorne 1967). Another hybrid, *Q. macdonaldii* (*Q. dumosa* x *Q. lobata*), a winter deciduous species, occurs as solitary trees or as hybrid swarm populations grading with *Q. dumosa* in many areas of both islands, particularly in wetter sites. All stands, however, are too small to be mapped.

The endemic *Lyonothamnus floribundus* forms small, compact groves, mostly in dry portions of canyons. It is widespread on Santa Cruz Island; 412 known groves, covering 300 hectares, occur throughout the island, except at the isthmus and on the warm, eastern half of the interior central valley. On Santa Catalina, 40 groves, covering only 30 hectares, are concentrated along the wettest portions of the channel slope from Avalon west to Long Point.

A few madrone (*Arbutus menziesii*) are reported along a watercourse on the channel slope of northwest Santa Cruz Island.

Riparian Woodland

In spite of the presence of some perennial streams, riparian vegetation on these islands is remarkably impoverished. The only taxa abundant enough to be mapped are *Salix* spp., *Populus fremontii*, and *Baccharis glutinosa*, all characterized by wind-borne seed. Heavy-seeded mainland riparian trees are quite rare or absent. *Platanus racemosa* was introduced to both islands in the early 20th century. *Alnus rhombifolia* and *Acer macrophyllum* are conspicuously absent. One *A. macrophyllum* occurring in a gully west of Prisoners Harbor was probably planted.

The geographic extent of riparian vegetation reflects the climatic differences between the islands. On Santa Catalina, this association is highly localized and consists largely of *Salix* thickets. One *P. fremontii* population occurs in lower Middle Canyon. Santa Cruz supports about 20 *P. fremontii* groves, several of which are long gallery forests along streams. *Salix* spp. often forms impenetrable stands where there is permanent water, while *Baccharis glutinosa* occurs along dry washes, especially those draining severely eroded portions of the island (notably the interior central valley, Laguna Canyon, and an unnamed drainage leading to Willows Anchorage on the south coast).

Closed-cone Pine Forest

Pinus muricata forests cover mostly north-facing slopes in three areas of Santa Cruz Island: the east half of the isthmus ridge, the channel slope just west of Prisoners Harbor, and several drainages leading to the Christi Ranch on the west end. The latter stand also extends southward along a sharp ridge to Sierra Blanca. Most populations are small and discrete. An impressive stand, however, covers more than 100 hectares in the upper headwaters of Cañada Cervada. The floristic composition and physiognomy of *Pinus muricata* forests varies considerably depending on grazing pressure (Hobbs 1980). Along the isthmus ridge and the west end, protected forests are contiguous, contain abundant pine reproduction and ground litter, and are admixed with a broken cover of a number of shrubs, including *Heteromeles arbutifolia, Arctostaphylos confertifolia, A. tomentosa, Vaccinium ovatum, Comarostaphylis diversifolia*, and prostrate *Quercus wislizenii*. Grazed forests on Sierra Blanca and west of Prisoners Harbor are open, contain few shrubs, and are lacking in reproduction except for toxic herbs such as *Eremocarpus setigerus*. The overall distribution of *P. muricata* is limited to sites exposed to maritime influences to the north and west, and to elevations where the marine layer is most frequently condensed as stratus during the summer (300 to 500 m), suggesting that this species may depend on summer stratus and fog drip to ameliorate drought stress.

ISLAND-MAINLAND VEGETATION AFFINITIES

In spite of their proximity to the southern California mainland, the vegetation of Santa Catalina and Santa Cruz Islands is strikingly different from the vegetation on nearby coastal mountain ranges, such as the Santa Ynez and the Santa Monica Mountains. This is surprising if one expects that similar environments near one another should have similar vegetation. This generalization holds true only to the level of species dominance. The vegetation data presented here reveal that species contributing most to island plant cover are also important mainland dominants. Present grasslands consist of exotic European annuals that also cover most of coastal California. The dominant species of coastal sage scrub are the familiar *Artemesia californica, Salvia apiana*, and *S. mellifera*. Among the chaparral, a few dominants endemic to the Channel Islands, or having limited distributions along the California coast, include *Arctostaphylos insularis, A. subcordata*, and *A. tomentosa*. Other species are not only significant mainland shrubs, but their distributional relations in the complex terrain of the Islands are much the same as those described for the coastal mountains of southern California (Hanes 1971). Oak woodlands contain two species endemic to the Channel Islands, *Quercus tomentella* and *Q. macdonaldii*, but most stands are dominated by *Q. agrifolia*, widespread from coastal central California to northern Baja California. Finally, the closed-cone pine, *Pinus muricata*, is found intermittently along a large stretch of the west coast from northern California to northern Baja California. The most notable endemic is *Lyonothamnus floribundus*, but it has a very localized distribution on the islands.

Major differences between island and mainland vegetation become apparent when one examines the physiognomy and geographic extent of the dominant plant communities. The strangest aspect of island vegetation is the generally oversized, arborescent appearance of chaparral shrubs and the open configuration of stands. An additional, related anomaly is the relative unimportance of woody vegetation and the widespread extent of grasslands. Grasses cover not only the heavier loams but also shallow rocky soils; these savannas, together with the shrub and woodland species, are reminiscent of the coast ranges of central California, rather than the solid brushfields covering southern California mountains.

Although many researchers have attributed these trends to the ameliorating influences of a cool, equable climate (Philbrick 1967), a more tenable explanation for these differences is believed to be long-term overgrazing by feral animals, particularly sheep and goats, which annually denude or damage the vegetation and disrupt normal plant life cycle processes. Grazing has also indirectly modified the natural fire regime due to the continual "harvest" of flammable brushland fuels. Although the Channel Islands are more exposed to maritime influences than are most mainland areas, they are still subject to summer drought, desiccation of vegetation, and the potential of fire. Historical accounts from before the turn of the present century, when fire suppression was begun, leave no doubt that fire was once widespread throughout coastal southern California (Minnich 1978). Fires ignited by lightning, Indians, and early European settlers apparently spread at will for long periods of time, perhaps weeks or months, until extinguished by fog or the first autumn rain. The fire regime on the islands could be considered in the context of natural and man-caused ignitions. However, fire is more a product of the physical environment, characterized by a tremendous imbalance between plant productivity and decomposition rates, and the accumulation of highly flammable fuels (Specht 1969, DeBano *et al.* 1977). How fires began in the past, and how extensively and frequently they spread, will probably never be known. Instead, it is important to recognize that fire is a natural part of the life cycle of this type of vegetation. The presence of numerous shrub species with survival strategies linked to fires gives strong evidence for the long-term role of fire on the islands.

The persistence, geography, and gigantism of present brush and woodland communities can be partly explained in terms of the relative tolerance of different species to browsing, and their ability to persist in the absence of fire. The resilience of a species to grazing is clearly a function of its size and height; feral animals browse almost all available vegetation within their reach. By late summer, annual grasses have been eaten, but these regenerate the following spring from seeds lying in the soil. Coastal sage scrub species are not so fortunate. Their limited size also virtually guarantees their destruction. The fact that coastal sage scrub is limited to areas protected from feral animals suggests that grazing may inhibit regeneration over large portions of both islands. Indeed, some areas of coastal sage scrub recently closed to goats or sheep have recovered, but very slowly. It is interesting to note that on south Santa Cruz Island most recovered areas are *Artemisia californica,* which are capable of long-distance wind dispersal. Interior portions of eastern Santa Catalina Island protected from goats in the 1950s are being rapidly invaded by *Artemisia californica, Salvia apiana,* and *S. mellifera* (Fig. 3). The survival of *Salvia,* which relies on seed storage, local dispersal, and disturbance for reproduction, was probably enhanced by widespread protective *Opuntia* thickets. Survival of *Salvia* and other locally dispersed species might also have occurred on Santa Cruz Island, were it not for the introduction of the cochineal insect to eradicate *Opuntia*.

Feral grazing is probably the primary factor for the gigantism and openness of the chaparral (Fig. 3). Shrubs experience so few fires that they are not forced to regenerate by sprouting or by seeds, as they do frequently on the mainland. Moreover, the shrubs are annually "pruned" by grazing, forcing crowns to grow taller than if left undisturbed. Stands thin out due to the combination of adult attrition and lack of reproduction. Most shrubs in heavily grazed areas are probably relicts of the pregrazing period.

Species selection due to long-term overgrazing may also explain some of the present floristic composition of the chaparral. The largest species, *Quercus dumosa*, *Heteromeles arbutifolia*, *Arctostaphylos* spp., and *Malosma laurina*, should survive best, particularly on mesic, north-facing slopes where, as a result of greater moisture availability and plant growth, these species send leaves beyond the browse line more quickly than do plants on drier slopes. Conversely, the possibility that frail *Adenostoma fasciculatum* and *Ceanothus megacarpus* would be more rapidly eliminated than other shrubs may account for their absence on the islands. As a current demonstration, the best stands of *Adenostoma fasciculatum* in goat- and pig-infested areas west of the Santa Catalina isthmus have rapidly thinned out in the last three years, during which time *Heteromeles arbutifolia*, *Quercus dumosa*, and *Rhus integrifolia* have held their own.

By virtue of their size, woodland species and *Pinus muricata* have probably suffered the least mechanical damage from feral animals, as is suggested by their distribution even in the most heavily grazed areas.

The elimination of fire would also be deleterious to chaparral species with fire-related survival strategies. Chaparral may be loosely divided into two classes whose strategies are highly divergent (Wells 1969). One group is characterized by long-lived species which have fleshy fruits that are consumed by animals, and seeds that may be dispersed over great distances. Such plants exhibit continuous reproduction between fire disturbances and recover from fire primarily by sprouting, an ancient trait common to angiosperms whether in flammable or nonflammable habitats. Examples include *Quercus dumosa*, *Heteromeles arbutifolia*, *Malosma laurina*, and *Rhus integrifolia*. The other group, which consists of *Adenostoma fasciculatum*, *Ceanothus* spp. and *Arctostaphylos* spp., exhibits seed dormancy and reproduces *en masse* after fires by seed scarification; the abundance of species in this group is stimulated by burning (Horton and Kraebel 1955, Patric and Hanes 1964, Hanes 1971). In the absence of fire, chaparral succession develops by an ascendancy of long-lived shrubs over short-lived ones (Hanes 1971). Santa Cruz and Santa Catalina Islands seem to be an extreme case of this condition; *Ceanothus* spp. and, to a lesser extent, *Adenostoma fasciculatum* have a short life span and poor reproduction due to both the lack of fire disturbance and to grazing. It is curious that the island chaparral most closely resembles petran chaparral found on the desert margins of the southern California coast ranges (Hanes 1971). Both plant communities are dominated by the same long-lived genera, including *Quercus*, *Cercocarpus*, and *Arctostaphylos*, in stands of tall, widely-spaced shrubs. Both experience fire frequencies too low to select for species with fire strategies, in one case due to a dry climate (low productivity), and in the other due to feral animal grazing.

Ironically, fire would be a death knell to woody vegetation under the present grazing regime. Shrubs will still not be able to reproduce and sprouts will be destroyed because they must regenerate within browse range. Only thick-barked pine and woodland species could survive, either by directly escaping combustion or by sprouting above the browse line.

Given the indiscriminate burning practices of 19th-century European livestock grazers in southern California (Minnich 1978), it is not at all improbable that much chaparral was removed by fire and grazing during the past hundred years. This is suggested by early ground photographs which show heavy brush vegetation on presently denuded slopes on both Santa Cruz (see Brumbaugh 1980) and Santa Catalina (Fig. 3). Moreover, these photographs reveal chaparral physiognomy reminiscent of mainland stands, *i.e.*, contiguous cover and a low homogeneous height profile indicative of earlier burns. Browse lines and arborescence are absent. The similarity of the vegetation as recorded by vertical aerial photography both in 1929 and at present indicates, however, that the bulk of vegetation damage due to grazing and fire

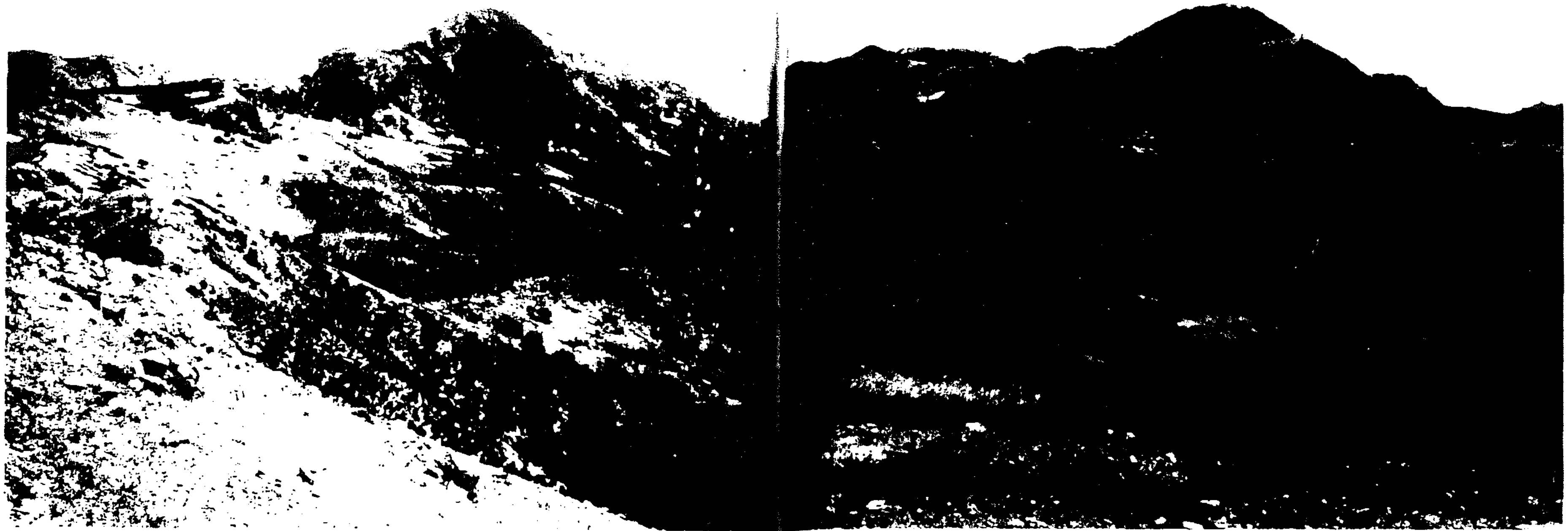

FIGURE 3. *Views of Mt. Black Jack from the present airport site in central Santa Catalina Island taken in the 1880s (left) and the present (right).* **Left:** *Continuous low shrub matrix evident in the mid-ground and on the north slope of Mt. Black Jack is primarily* Adenostoma fasciculatum *interlaced with numerous goat trails. Larger shrubs embedded with* Adenostoma fasciculatum *and with grassland to the left and in the foreground are mostly* Quercus dumosa *and* Malosma (Rhus) laurina. *Note the browse lines on several individuals in the center left. Huntington Library Photo Collection, Pierce 4195.* **Right:** Adenostoma fasciculatum *has nearly disappeared and is replaced by grassland and an open stand of* Quercus dumosa *and* Malosma (Rhus) laurina, *of much larger size than in the earlier photograph. These shrubs have also increased in abundance. Subshrubs in the center left are coastal sage scrub dominated by* Artemesia californica *and* Salvia apiana, *which invaded the area after goats were removed in the 1950s. According to A. Douglas Probst, thousands of dead* Adenostoma fasciculatum *burls were picked up by Avalon citizens throughout the island for use in barbecues until the practice was stopped by the Santa Catalina Island Conservancy about 20 years ago. Photo by A. Douglas Probst.*

occurred before the turn of the century.

In contrast, cursory analysis of numerous ground photographs of Avalon Bay in eastern Santa Catalina Island (Huntington Library Photo Collection) shows dramatic increases in woody vegetation due to urbanization, attendant declines in browsing pressure, and fire protection. An overgrazed landscape of sparse grass, *Opuntia*, and open, pruned chaparral in the 1880s developed rapidly into coastal sage scrub by 1900 after the resort town was established. Thereafter, chaparral dominated by faunal-dispersed species, notably *Heteromeles arbutifolia* and *Rhus integrifolia*, have invaded at a slower pace, becoming conspicuous on photographs after about 1940. Such recovery would be expected over much of these islands if feral animals were removed. Present fire protection, on the other hand, is resulting in a serious wildland fire problem at Avalon.

CONCLUSION

Because most woody plant communities have not been able to reproduce over large areas of Santa Cruz and Santa Catalina Islands over a long period of time, one cannot assume that the present vegetation described here represents prehistoric conditions. On a global scale, forests and shrublands in many areas have been converted into savannas or grasslands due to excessive disturbance, mostly as the result of human activities. Among these vegetation transformations, evergreen sclerophyll scrub has been degraded by centuries of overgrazing and burning in several Mediterranean ecosystems (Naveh 1977, Susmel 1977, LeHouerou 1977). Similarly, Santa Catalina and Santa Cruz Islands probably supported widespread brushland vegetation before the introduction of domestic animals. For reasons given above, the plant communities which probably declined the most include coastal sage scrub and chaparral dominated by *Adenostoma fasciculatum* and *Ceanothus*. If one imagines the addition of large areas of these plant communities to areas with existing (and probably aboriginal) woody cover and, in particular, the replacement of grasslands on poor rocky sites, the removal of feral animals, and the burning of vegetation with some regularity, the resulting picture of prehistoric vegetation on these islands should be much like that now observed in any mountain range in coastal southern California.

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