

CHAPTER III

CLIMATE, STRUCTURE, AND HISTORY
OF CALIFORNIA'S ANNUAL GRASSLAND ECOSYSTEM

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The California annual grassland ecosystem is a composite, discontinuous plant community embracing open treeless grasslands and continuous and intermingled woodlands. It is constituted of three grassland communities, variously termed valley grassland, coastal prairie, and California prairie; and of three woodland communities, referred to as foothill woodland, northern oak woodland, and southern oak woodland. While geographically extensive and somewhat disjunct, the essential unity of the ecosystem is attested by its distinctive climatic features and physiographic similarity throughout; and by the dominantly herbaceous annual life form of its vegetation, as well as the physiological and phenological responses of the vegetation to factors of the environment.

Geographically, the annual grassland occupies the margins of the Central Valley and the adjacent foothills of both the Sierra Nevada and the Coast Ranges. It includes the low, hot interior valleys--such as Salinas, San Benito, and Antelope valleys--of the South Coast Ranges, together with their surrounding woodlands. It extends southward through the coastal areas from San Luis Obispo County to San Diego. The coastal prairies, scattered grasslands, and intermingled open woodlands of the middle and outer North Coast Ranges, from San Francisco Bay northward into Humboldt and western Trinity counties, are also part of the plant community thus broadly delimited. It extends north and south through about 8 1/2 degrees of latitude, and is some five degrees of longitude from east to west.

Physiographically, the grassland elements of this ecosystem occur on gently undulating open plains and low terraces of the valley floors. They extend upward onto moderately rolling to hilly topography bordering the valleys. They also occupy much of the more level land--swales and stringers--within the woodlands. Woodland portions of the ecosystem are characteristically on more rolling to hilly terrain. In elevation, it lies mainly between sea level and about 3,000 feet, but fingers upward to about 5,000 feet in southern California and on warm slopes in the north.

CLIMATIC TYPES

The Central Valley and its surrounding foothills and the South Coast Ranges have a dry-summer subtropical climate. This climate is characterized by a high percentage of sunshine in all seasons; by dry, warm-to-hot summers; and by mild, rainy winters. Since these conditions prevail also in the regions around the Mediterranean Sea, this kind of climate is often referred to as the Mediterranean, or Mediterranean subtropical, climate. The climatic type known as "Mediterranean" is, in fact, a family of climates, more than one of which occurs in California. About 57 per cent of the state is dominated by this climatic type. Four other regions of the world also have Mediterranean climates.

The middle and outer North Coast Ranges, from San Francisco Bay northward, have a mesothermal marine climate characterized by mild winter, cool summers, and higher rainfall. Its proximity to the ocean and to prevailing on-shore winds make this one of the most equable of climates.

For the annual grassland ecosystem, as for California as a whole, major climatic controls are exerted by latitude, the influence of the Pacific Ocean, and the orientation and extreme range in elevation of the topography, with the last by far the most important (Byers, 1931). Contrary to the usual situation, where latitude is a major determinant of temperature differences, in California the effect of latitude is only minor and is subordinated to that of topography.

Because of its great geographical extent and the significant differences in elevation, there are correspondingly large variations in climatic elements for the grassland ecosystem. Mean maximum temperatures are from 63° to 102° F in summer, and winter minima are from 29° to 45° F. The growing season varies from six months (in the more northerly portions and at higher elevations) to the entire year (in the south). The frost-free period may be as short as 175 days, or as long as 365 days.

Average annual precipitation ranges from 6 inches (in the south) to more than 75 inches (in the northern coastal regions). Practically all precipitation comes during winter, at irregular intervals; it is principally from storm systems generated in the North Pacific Ocean. A major part of it is received as rain, with snow being of limited importance in the inland portions at higher elevation.

An important climatic factor for the vegetation is fog, which is most frequent in coastal and neighboring foothill districts. It increases generally with latitude, and with altitude up to some 2,000 to 3,000 feet. Along coasts and windward slopes it is more frequent in summer than in winter. In winter, fog may be more important in inland areas, including the Central Valley.

Throughout the Central Valley, and in some coastal valleys as well, there are frequently periods of from a few days to more than two months in winter with a temperature inversion under a static or stagnant high-pressure area. At such times, a thick layer of fog forms which may be from less than 500 to as much as 2,000 feet thick. Temperatures then have a narrow diurnal range, sometimes as little as two to four degrees F; there is little wind movement. At these times, a wide band around the edge of the valley is swathed in fog. These winter fogs may occur between late November (after the first significant rains) and early April, but are more prevalent between December and March.

STRUCTURE OF THE VEGETATION

Under the climatic regime prevailing throughout the annual grassland ecosystem, herbaceous plants are dominant. Both grasses and forbs are strongly represented. Grasslike plants (sedges and rushes) are usually present in small numbers, especially in swales and similar more moist areas. These herbaceous annual plants begin growth in fall, the seed germinating after the first "effective rain"--amounting to about one-half inch in a single storm (Bentley and Talbot, 1951). They grow slowly through late winter, the rate of growth depending on weather conditions. The brilliant greens of grasses in the winter season are a vivid contrast to the parched brown landscape of the long, dry summer. The annual vegetation matures by late March or early April in the south; by June in the north. Seed is scattered, and the plants dry up, becoming bleached by the sun and occasional summer rains.

The woodland portion of this ecosystem is a composite community of trees, shrubs, and open grasslands. Trees may be intermixed with shrubs in very open to dense stands, with a total crown cover of woody vegetation ranging from only two or three per cent upward to nearly 100 per cent. In general, tree-herb and tree-shrub-herb subcommunities predominate. Trees are primarily oaks (Quercus); Digger pine (Pinus sabiniana) is the most common associate; California buckeye (Aesculus californica) and others are less frequent. Shrubs are mainly various kinds of Ceanothus, Arctostaphylos,

and Rhamnus. Woody plants of this community tend to be small, with waxy small leaves, mainly evergreen, and often with thick bark. They are usually widely spaced; have very deep or widely spreading root systems; and are adapted in various ways to the long rainless summers.

Throughout the grassland ecosystem herbaceous annual plants are the dominant vegetation life form. They are a strong element even where aspect dominance is maintained by open woodlands, commonly forming essentially a continuous ground cover under all but the densest stands. The original perennial bunchgrass dominants have long been superseded by annual brome-grasses (Bromus), fescues (Festuca), wild oats (Avena), and a long list of others (Burcham, 1957; 1961). Associated with the grasses is a host of forbs, both native and introduced, the most common and widespread being filarees (Erodium); a variety of legumes--bur clovers and true clovers (Medicago and Trifolium), lupines (Lupinus), and trefoils and deervetches (Lotus); and tarweeds (Hemizonia and Madia) and similar late summer annuals.

For the annual grassland ecosystem as a whole the most ubiquitous and abundant plant is soft chess (Bromus mollis). This grass was found in all but one of 38 stands sampled from Sacramento to Madera County in the Sierra foothills and from Santa Clara to Monterey County in the South Coast Ranges (Table 1). In terms of percentage of herbage cover it was the most abundant species in 30 of these stands. Filarees were the second-most important group of plants in terms of both constance and abundance, occurring in 31 of the stands sampled, and being most abundant in 28 of them. Annual fescues, principally Festuca megalura, had a constance value of 50 per cent,

Table 1. Constance and abundance of selected plants in thirty-eight stands of annual grassland.

Species	Constance		Abundance*	
	Number of plots	Per cent of plots	Number of plots	Per cent of plots
<u>Grasses</u>				
<u>Avena</u>	16	42.1	3	7.9
<u>Bromus madritensis</u>	1	2.6	0	---
<u>Bromus mollis</u>	37	97.4	30	78.9
<u>Bromus rigidus</u>	21	55.3	1	2.6
<u>Bromus rubens</u>	9	23.7	0	---
<u>Festuca (annual species)</u>	19	50.0	4	10.5
<u>Hordeum</u>	10	26.3	4	10.5
<u>Forbs</u>				
<u>Brodiaea</u>	3	7.9	0	---
<u>Erodium</u>	31	81.6	28	73.7
<u>Hemizonia</u>	7	18.4	2	5.3
<u>Hypocheris</u>	4	10.5	0	---
<u>Lotus</u>	3	7.9	0	---
<u>Medicago</u>	4	10.5	3	7.9

*Based on estimated percentage of forage cover of each species on sample plot.

occurring in 19 of the stands. In abundance, they were equaled by the wild barleys. Ripgutgrass (*Bromus rigidus*) exceeded the annual fescues in constance but was very low in abundance in these stands.

Native forbs have maintained a much stronger position in the annual grassland flora than have the grasses. Their abundance and variety cause these grasslands to vary markedly in appearance with the progression of the seasons, probably without parallel in any other California plant community. At certain times of the year, from early spring into mid-summer, a given species--or a group of species--may be so conspicuous as to obscure the grasses, creating the illusion of being the dominant vegetation. In this respect, the appearance of these grasslands is frequently reminiscent of descriptions left by early travelers in these regions (Cronise, 1868; Muir, 1911).

The dominance of these seasonal societies and the plants which constitute them vary from year to year, reflecting differences in the amount and seasonal distribution of rainfall, prevailing temperatures, and other weather elements, as well as season of use and intensity of grazing.

DISTINCTIVE FEATURES OF THE CALIFORNIA ANNUAL GRASSLAND ECOSYSTEM

The magnificent forage resource found in California by the early Spanish settlers differed from that of any other range region of North America in a number of ways: in climatic conditions; in composition of the forage cover; and in ecological characteristics and physiological responses of the flora.

The climatic conditions under which the California grasslands developed are distinctive. California grasslands receive their precipitation in winter, essentially all of it as rain. East of the Rocky Mountains, the Great Plains grasslands receive some snow in winter, but their maximum of precipitation is in summer during the growing season. Even the Palouse Prairie of southeastern Washington, which has its major precipitation in winter also, receives some summer rainfall; and year-around temperatures are lower. The distinctiveness of the climate of the California grassland ecosystem is illustrated dramatically when the composite hythergraph for this region is compared with those of the Great Plains grasslands (Smith, 1940), as is done in the model (Fig. 1).

The California prairie--and the grassland elements of contiguous woodlands as well--were distinguished from related floral units of the Pacific Northwest, and from grasslands of the Great Plains by the number and importance of annual plants, and particularly of forbs, in the plant cover (Beetle, 1947). In fact, in some situations annual plants must have been dominant locally. In addition, while many of the genera and some species characteristic of other North American grasslands were represented in the California prairie, most of the dominant species have relatively restricted distributions elsewhere. Finally, the sod-forming grasses, important floristic elements of grasslands east of the Rocky Mountains, were virtually absent from California grasslands.

The fact that California's summer drought is followed by a winter season of comparatively high precipitation has important bearings on the ecological characteristics and physiological responses of the range forage. Plants growing in regions of Mediterranean climate must be adapted to an extremely great range in habitat conditions, especially with respect to heat and moisture, as illustrated in the accompanying model (Fig. 2). They must be able to make appreciable growth during winter, when temperatures are low and soil moisture is at or near saturation levels, with consequent poor soil aeration. In summer, these plants must survive or evade deficiencies of soil moisture, and temperatures comparable with those of the desert.

In California grasslands the period of active growth begins in fall, with the onset of shorter days and lower temperatures. Annuals germinate after

the first effective rains, but perennial grasses quite commonly begin growth before fall rains occur (Burcham, 1957; 1961; 1970b). This early growth by perennials depends upon food reserves stored in the root; grazing practices must provide for their replenishment if perennials are to be maintained in the stand. Annuals evade summer drought by maturing seed at the beginning of the dry season; perennials by dormancy. These and related characteristics are major elements in the explanation of what happened to California grasslands under grazing, especially during the first century of use.

GRAZING ON CALIFORNIA GRASSLANDS

Domestic livestock began grazing on California grasslands more than two hundred years ago. The Spanish colonists who founded the first settlement at San Diego in 1769 brought cattle and other livestock with them. Nourished by the excellent forage of the California range lands, the animals thrived, providing many necessities for the new colony. This first settlement was soon followed by others; additional livestock were brought to the province. The livestock industry that developed as settlement progressed constituted the economic foundation of Spanish California until gold was discovered, in 1849. Ranching has continued to maintain its prominence: today it is the most widespread agricultural activity in the state; and for years it has been the foremost agricultural commodity in terms of income produced.

Four phases of ranching can be identified as California progressed from a frontier outpost of New Spain into the Twentieth Century (Burcham, 1961). Development of ranching was accompanied by significant changes in both the area and character of the grazing lands.

Ranches of the Spanish missions dominated the Californian scene from the beginning of settlement until about 1833. Additional missions followed the first one, at San Diego, in rapid succession. By 1823, a chain of 21 missions extended along the coast from San Diego to Sonoma. Ranches of the missions occupied most of the lands in the coastal region held by the Spaniards, about one-sixth of the total area of the state. Probably more than 400,000 cattle and 300,000 sheep grazed on this pastoral empire of the missions (Robinson, 1948). Missions were colonizing agents of the Spanish government, and were not intended to be permanent.

After the mission lands were transferred to the civil government, between 1833 and 1836, liberal grants of land were made to private individuals as an incentive to engage in ranching or agriculture. These Mexican ranchos (Mexico had won her independence from Spain in 1822) succeeded the mission ranches. Operated by private enterprise, they were the centers of ranching activity from the mid-1830's until 1850.

Early American ranches--supplying local demands for animal products, and as speculative ventures--prevailed from about 1850 until the middle 1860's. Discovery of gold in California created an unprecedented market for meat--almost immediately, and literally at the rancher's doorstep. Large quantities of meat were needed in the various mining communities and in the rapidly growing metropolitan centers of San Francisco, Sacramento, and Stockton. A strong demand for meat and an extremely limited local supply of cattle led to major movements of livestock into California from Mexico, Texas, and the Middle West. These conditions also promoted intensive speculation, especially in the cattle industry. Alternating periods of drought and high rainfall in the 1850's and early 1860's wrought havoc with the livestock industry. Hundreds of thousands of animals were drowned in widespread floods in the winter of 1862; and in the next two years possibly a million head died from drought. These drastic consequences of flood and drought permanently curbed cattle ranching on a speculative basis in California. The experiences of that period, however, led to the first positive steps in range improvement and better animal husbandry.

Demands of crop agriculture made the first major inroads upon the open

range between 1860 and 1870, which has been characterized as California's "Decade of Wheat" (Wickson, 1923). Great acrages of valley land were diverted from range to wheat production. This period of agriculture and adjustment, from about 1865 until well past 1880, was the fourth phase in the development of livestock ranching. As settlement of the state proceeded and emphasis on farming increased, the era of cheap, free range for livestock was ended in the valleys and certain portions of the foothill country. The pastoral industry shifted to the upper margins of the grasslands and the woodland ranges of the foothills, and to the plateau and mountain portions of the state, where it became essentially stabilized.

CHANGES IN THE GRASSLANDS

Two centuries of grazing and agriculture in California have greatly altered both the extent and character of the grasslands. Approximately 14 million acres of the state are now under cultivation or occupied by urban and industrial areas. The greater part of this area--probably as much as 12 million acres--was originally in the California prairie and woodland plant communities, and hence was predominantly grasslands.

Within the grasslands which remain, the most striking change has undoubtedly been replacement of the native perennial grasses by annual plants, a large proportion of them introduced from the Mediterranean region of the Old World. Few places on earth, if any, have had such a rapid large-scale replacement of native herbaceous vegetation by alien plants. To a large degree it was accomplished within 20 years (between 1845 and 1865), but the process began almost as soon as the first settlement was founded, and it continues even today.

The many crop and garden plants brought to California by early settlers were not of consequence in replacing native vegetation of the grasslands. Plants important in this connection were introduced unintentionally, almost without exception. They came mostly as "hitch-hikers": in packing materials; as impurities in cultivated crops; in ballast; even in the coats of domestic animals. Early accounts confirm widespread distribution of alien plants at a comparatively early date. At least 95 important aliens--mostly annuals--were fairly well established by 1860, with grasses and composites being most numerous (Robbins, 1940).

PLANT SUCCESSION IN THE ANNUAL GRASSLAND ECOSYSTEM

Some of these introduced plants--chiefly grasses--became dominant over great areas of California grassland during rather definite periods, in chronological sequence. Four stages of plant succession which were of major significance in replacing the native perennials by annual plants have been identified (Burcham, 1957); they are illustrated in the accompanying model (Fig. 3). The first stage was characterized by wild oats (*Avena*) and black mustard (*Brassica nigra*); it was most prominent between 1845 and 1855. Filarees (*Erodium*), wild barleys (*Hordeum*), nitgrass (*Gastridium ventricosum*), and native annuals represented by foxtail fescue (*Festuca megalura*) composed the second wave of succession, which was dominant from about 1855 until 1870. Plants such as mouse barley (*Hordeum leporinum*), red brome (*Bromus rubens*), silver hairgrass (*Aira caryophyllaea*), Chile tarweed (*Madia sativa*), and star thistle (*Centaurea*) were representative of the third stage; it began during the 1870's and is widespread on California grasslands today. A fourth stage, beginning about 1900, is now well established; it is constituted of alien annual grasses--represented by medusa-head (*Taeniatherum asperum*), barb goatgrass (*Aegilops triuncialis*), dogtail grass (*Cynosurus echinatus*), and annual falsebrome (*Brachypodium distachyon*)--and of forbs such as *Hypochoeris*, *Navarretia*, *Eryngium*, and other native and introduced species.

This chronological sequence in dominance of the grassland cover corresponds

to the descending scale of annual plant succession. It also indicates a decline in productivity, and reflects intensity of grazing use.

Superficially, the range lands of California did not differ in appearance from many eastern grazing lands. Early ranchers stocked and managed them according to practices with which they were familiar. But the forage cover was deceptively lighter than on grasslands having summer rainfall; production was not renewed through the growing season by abundant rains; and ecological responses of plants of Mediterranean regions to grazing are distinctly different. Disturbances of the plant cover of the grasslands, by grazing and other activities, favored vigorous responses of native annual plants of inferior quality--and of introduced grasses and forbs. Range lands with these characteristics may change strikingly under the impacts of grazing animals.

A major part of the explanation for the changes lies in the adaptations of the plants themselves to the distinctive environmental conditions of Mediterranean lands. These plants evolved in regions having climates similar to California, surviving for centuries on lands grazed heavily by domestic livestock, where all but the most aggressive genetic strains were eliminated (Burcham, 1957; 1970a). They are particularly adapted for distribution by seed. They have a wide range of adaptation to soils and other site factors. They germinate quickly under favorable conditions, grow rapidly, and mature quickly. Great quantities of highly viable seed are produced; a high degree of viability is retained by seed sowed naturally in litter and duff; the same is true of seed stored under only marginally favorable conditions even over a period of years (Burcham, 1957; 1970a). Finally, these plants compete effectively with other species and are able to maintain themselves even in unfavorable situations for periods of many years. These characteristics are held in common by most of our native annuals, as well as by the introduced species.

Largely because of their specialized adaptations and aggressive growth, and their tolerance for a wide range of habitat conditions, these alien plants and our native annuals have been able to transform the essential character of our grasslands. The changes in plant composition and vegetation structure have been accompanied by lowered productivity and reduced nutritional efficiency for livestock, resulting in ecologically significant shifts in biotic relationships of the plant-soil-animal complex.