Plant 39

Terrestrial Vegetation Of California
Edited by M.G. Barbour and J. Major
Wiley-Interscience 491-514

CHAPTER 14

VALLEY GRASSLAND

HAROLD F. HEADY
College of Natural Resources, University of California, Berkeley

THE CALIFORNIA PRAIRIE

Several names commonly apply to the low-elevation grasslands that lie west of the Sierra–Cascade crest and in southern California. Shantz and Zon (1924) mapped this grassland as the *Stipa–Poa* bunch grass type and classified it as part of the Pacific grassland. Clements (1934) called single-species stands along rights-of-way in the Central Valley the "*Stipa pulchra* consociation of the California bunch grass prairie." Numerous later authors and speakers refer to the area simply as the "California prairie" or the "California annual grassland" (Fig. 14-1). The first name emphasizes the perennial nature of the pristine grassland species, and the latter draws attention to the current dominance of annual plants; neither, however, attempts to divide the area into two or more parts.

Burcham (1957) and Munz and Keck (1959) described the California prairie as a valley grassland with southern affinities and a north coastal prairie with northern relationships. Küchler (1964) labeled these parts as California steppe and *Festuca–Danthonia* grassland, respectively. Although the names differ, general descriptions leave little doubt as to their synonymous nature. This chapter concentrates on the valley grassland; Chapter 21 discusses the coastal prairie.

The first accounts of the California prairie described it simply as excellent pasture. Perhaps the earliest vegetational study of consequence was made by Burtt-Davy (1902), who described grasslands in the north coast mountains. Reports before 1900 by explorers, survey parties, and botanical collectors provided some information about the kinds of plants in the grasslands, but these limited vegetational descriptions give us grist for continuing deductive arguments. For example, on April 1, 1868, John Muir wrote of Santa Clara Valley, "the hills were so covered with flowers that they seemed to be painted" (Adams and Muir 1948). On the same trip,

Figure 14-1. Grazed valley grassland with *Aesculus californica* in the foreground and *Quercus* behind.

Muir referred to the Central Valley as a "garden of yellow compositae." But that was early April, when *Baeria chrysostoma, Amsinckia intermedia, Eschscholtzia californica,* and others make their brief show on restricted habitats. Six weeks later the descriptions could well have suggested a sea of mixed grasses gently moving in the morning breeze. One could argue from these observations that the vegetation was either annual or perennial, or a mixture of both.

History has not recorded the vegetational dynamics of the pristine California prairie. After 25 yr of studying this grassland, I believe that plant succession tended toward perennial bunch grass dominants on nearly all well-drained upland sites, that numerous annual species were present, and that they dominated intermediate and low successional stages, just as they do in many other grasslands. Also, I believe that introduced annual plants prevent many perennial grasses from attaining their dominance, that annuals are now a large part of the climax on many sites (if not all of it), and that alien species should be considered as new and permanent members of the grassland rather than as aliens. Their elimination from the California prairie is inconceivable. These hypotheses will be examined in detail throughout this chapter.

Relation to Other Vegetational Types

The Palouse prairie, centered in eastern Washington and Oregon, is related to the California prairie because of closely similar floras and growth habitats of the dominants. Species such as *Festuca idahoensis, Koeleria cristata, Poa scabrella,* and *Sitanion hystrix* occupy dominant positions in both grasslands. These species gradually lose their importance from north to south and from the coast inland, thus forming a continuum between the Palouse prairie and the California prairie. The Palouse dominant, *Agropyron spicatum,* and the California dominant, *Stipa* *pulchra,* are not shared (Beetle 1947). In addition, Stebbins and Major (1965) claimed from genetic and paleobotanical evidence that many endemic species of the California prairie originated from northern ancestors.

A transition between the California prairie and the herbaceous vegetation in the desert scrub types of southeastern California occurs over a short distance on the eastern slopes of the Tehachapi and other southern California mountains. *Stipa speciosa* replaces the *Stipa* species of the California prairie, and species in the grass genera *Aristida, Bouteloua,* and *Hilaria* of the desert grassland occur sparingly except on north-facing slopes with coarse-textured soils, where they may form relatively dense stands. *Bromus rubens, Erodium cicutarium, Salsola kali,* and *Schismus arabicus* dominate the annual layer.

The valley grassland extends into oak woodland and chaparral with little change in its herbaceous characteristics. Large specimens of *Quercus lobata* may be found in the Central Valley and smaller valleys in the Coast Ranges. The gentle beginning slopes of the mountains bordering the Central Valley are covered with California prairie, but *Q. douglasii* gives the grassland a savanna aspect. Burcham (1957) suggested that the savanna appearance covered more area in pristine times than it does today.

The present-day valley grassland occurs as a ring around the Central Valley. Toward the center it irregularly borders cultivated land (mostly irrigated) and marshes or remnants of the once-extensive tule swamps, such as along the San Joaquin River in Merced and Fresno Cos. (Fig. 14-2). Poorly drained alkali soils occur most abundantly in the southern and western sides of the San Joaquin Valley, which lacks oceanic drainage. Bordering bare soil within the sinks, alkali-tolerant species such as *Allenrolfea occidentalis, Kochia californica, Salicornia subterminalis,* and *Suaeda fruticosa* occur. Grasses, such as *Distichlis spicata, Hordeum depressum,* and *Sporobolus airoides,* also characterize the type. With somewhat better drainage and on foothill areas. *Atriplex polycarpa* dominates and the annual

Figure 14-2. Marshland along the San Joaquin River in Fresno Co. This type has been reduced in area by drainage control and cultivation.

grassland species appear as an understory (Twisselmann 1967). A small area of *Artemisia tridentata* is also present. Inner coastal hills in San Benito Co. support *Atriplex polycarpa, Ephedra californica,* and *Haplopappus racemosus*. Some years in late March, *Monolopia lanceolata* turns the landscape to a bright yellow, whereas in other years *Erodium* and the annual grasses cause greens to dominate.

In marked contrast to the alkali flats, "hog wallows" on the eastern side of the Central Valley are small depressions that fill with fresh water during the rainy season. An endemic vernal flora has evolved around these pools.

Distribution

The pristine California prairie appears to have been little different in distribution from the present-day grasslands,except the areas taken for cultivation. Boundaries with woodland and chaparral may be less or more distinct because of man's activities, but it is doubtful that their relative locations have changed.

The original valley grassland covered well-drained areas from sea level to approximately 1200 m in all the mountains surrounding the Central Valley. The valley grassland occurs in scattered patches throughout the Coast Ranges, with the possible exception of the narrow fringe of coastal facing slopes from Santa Cruz northward. Küchler's (1964) map shows that 5.35 million ha support this grassland, and an additional 3.87 million ha have an oak overstory (area determined by planimeter).

Such a large area has many habitats, and few accurate generalities can be made as to typical conditions under which the grasses grow. Most grassland soils are noncalcic Browns, medium to heavy in texture, granular in structure, moderate in organic matter content, and often about 0.5 m in depth. The valley grassland occurs on a wide variety of soils, sometimes closely associated in a complex mosaic (Fig. 14-3). Barry (1972) listed 195 soils series on which the grassland might be found. Other vegetational types, especially oak woodland, also occur on most of them.

Average annual rainfall for the valley grassland ranges from about 12 cm in the southwestern San Joaquin Valley to 200 cm in northwestern California. Regardless of the annual amount, soil water deficits characterize the grassland habitat for 4–8 summer months every year. Although germination of seed and breaking of dry season dormancy for many perennials in the grassland follow fall rains, winters are cool, allowing little growth. Only in spring do warm temperatures, beginning about March, stimulate rapid growth, flowering, and maturity. Cool-season species mature from April to June, and a few warm-season annuals reach their peak growth in summer. Annual variations in weather greatly influence species composition and biomass production.

Composition of the Perennial Grassland

Stipa pulchra, beyond all doubt, dominated the valley grassland. Toward the southern end of the grassland, *S. cernua* increased in importance. Perennial grasses associated with *Stipa* were *Aristida hamulosa, Elymus glaucus, E. triticoides, Festuca idahoensis, Koeleria cristata, Melica californica, M. imperfecta,* and *Poa scabrella*. Annual grasses included *Aristida oligantha, Deschampsia danthonioides, Festuca megalura, F. pacifica,* and *Orcuttia* spp. Broad-leaved herbs included many

Figure 14-3. Grassland variations in stages of vegetational drying that are associated with soil differences.

perennials, especially plants with bulbs, and annuals in the Caryophyllaceae, Compositae, Cruciferae, Labiatea, Leguminosae, and Umbelliferae (Stebbins 1965).

Quantitative descriptions based on plot sampling of the relict perennial grasslands have not appeared. White (1967) gave indices of commonness for species in 17 stands of *Stipa pulchra* on Hastings Reservation in Carmel Valley. Only one perennial grass (*Stipa*) was found in those stands. Barry (1972) described 19 examples of the valley grassland where *Stipa* dominates and mentioned 20 other sites that he did not examine. None of his descriptions included data more quantitative than species lists. Burcham's excellent review (1957) of historical accounts of California rangelands contained many references to abundant water and excellent native pasture. Botanical collections began about 1830, long after grazing by domestic livestock had become extensive along the California coast, but no authors recorded the relative importance of the perennial grassland species.

Although the perennial grasses may be difficult to find, they have by no means been eliminated. Fence corners, roadsides, rights-of-way, and brush plants protect sites which frequently support *Stipa* and other former dominants of the pristine grassland. *Aristida hamulosa* may be the least common of these species. Barry (1972) recorded it abundantly only where Salt Canyon enters the Sacramento Valley in western Colusa County (NA 061915).

Originally the valley grassland probably appeared as a bunch grass prairie, similar to the Palouse prairie, with the exception that native annual species filled the interspaces between the large bunches of *Stipa*. In one exclosure on the Hopland Field Station, a canopy of *Stipa pulchra* covers the soil, but many annual plants still remain. White (1967) mentioned 68 of these subdominant species in *Stipa* stands with 11% basal cover on Hastings Reservation. Of the 68, 71% were native species. On shallow soils, a thin or scattered perennial stand permits numerous annuals to

C—057443

C-057443

increase in abundance. Annuals may dominate completely on certain sites, for example, the hog wallow communities at Dozier (Lin 1970; Luckenbach 1973).

REPLACEMENT OF THE PRISTINE GRASSLAND

Permanent alterations in the pristine grassland began when Europeans first reached the Americas. These changes resulted from a combination of (1) invasion by alien plant species, (2) changes in the kinds of animals and their grazing patterns, (3) cultivation, and (4) fire. Many authors suggest the relative importance of these factors by the order of listing above, but others believe that overgrazing was the principal destructive factor. That hypothesis has not been proved, nor can it be until something similar to the pristine grassland can be attained through separation and manipulation of each of the four factors. The following discussion takes them separately for reasons of simplicity, although their interacting impacts unquestionably changed the grassland.

Invasion by Alien Plants

Hendry (1931) suggested that *Erodium cicutarium, Rumex crispus,* and *Sonchus asper* may have preceded Europeans to California. Adobe bricks used to build the earliest Spanish missions contained these as well as *Hordeum leporinum, Lolium multiflorum,* and *Poa annua,* all introduced species. The earliest European arrivals to the Americas (Columbus, Cortes, Magellan, Coronado, and others) did not settle in California. However, seeds in packing and hay from Spain and in the debris associated with livestock on their sailing vessels undoubtedly were the sources of the alien plants. A brief land exploration, especially one with horses, from the first sailing vessel to reach the California shores probably left new plants. Many of the early ships carried a few live animals for meat; thus seeds in the manure thrown overboard could have resulted in alien plants reaching shore even though the sailors did not. Once a plant species produced seeds anywhere in the continent, birds could have carried them to other locations. California lies in the path of many bird migrations, especially north–south routes with one terminus in Mexico.

Burcham (1956, 1957) and Robbins (1940) presented evidence that suggests major replacement of the perennial grasses with introduced annuals in stages beginning in the 1850s. At that time, there appeared to be overgrazing in the coastal areas, and miners from all over the world had traveled to the gold fields, bringing seeds, bulbs, and cuttings of many plant species. Eleven years of drought caused much barren land. Perkins wrote in 1864, "Less than ten years ago, the traveller would ride for days through wild oats tall enough to tie across his saddle, now dwindled down to a stunted growth of six or ten inches, with wide reaches of utterly barren land," (as quoted in Burcham 1957). This statement suggests that *Avena fatua* and probably *Brassica nigra* invaded the Central Valley and became dominant before livestock had overgrazed the area. Similar botanical composition may be seen almost every year in the spring along the roadsides in the San Francisco Bay Area.

The second stage, about 1870, was dominated by *Bromus* spp., *Erodium* spp., *Gastridium ventricosum,* and *Hordeum leporinum.* Introduced annuals in the third stage, the 1880s, included *Aira caryophyllea, Bromus rubens, Centaurea melitensis,* *Hordeum hystrix,* and *Madia sativa.* A fourth group, *Aegilops triuncialis, Brachypodium distachyon, Chondrilla juncea,* and *Taeniatherum asperum,* has increased recently. Species not in California, such as *Cryptostemma calendula,* or cape weed in Australia, dominate Mediterrean-type grassland in other parts of the world. They have the potential to become part of the California annual grassland. Today *Bromus mollis,* which arrived about 1860, is the matrix species through much of the grassland, but it may not continue in that role. Plant succession within the annuals will be described later.

Changes in Kinds of Animals

The well-drained soils covered with pristine valley grassland supported large numbers of pronghorn antelope (*Antilocapra americana*), deer (*Odocoileus hemionus*), jackrabbit (*Lepus californicus*), Beechey ground squirrel (*Spermophilus beecheyi*), kangaroo rat (*Dipodomys heermanni*), and pocket gopher (*Thomomys bottae*). The tule elk (*Cervus elophus nannodes*) used both the well-drained uplands and the marshland along the rivers. Antelope occurred in herds of 2–3,000, and elk in the hundreds. Several of these grazing animals developed into strains found only in the Central Valley, suggesting a lengthy association between the vegetation and the grazing.

As European man and his domestic animals rapidly increased in numbers in the 1850s, the larger wild animals diminished. Rodents remain numerous. Fitch and Bentley reported in 1949 that 25 pocket gophers, 4 ground squirrels, and 12 kangaroo rats on 1 ha of land would eliminate about a third of the forage. Batzli and Pitelka (1970) found that the meadow mouse (*Microtus californica*) significantly reduced plant height, ground cover, and standing crop in both the coastal prairie and the annual grassland. Bartholomew (1970) and Halligan (1973) reported that small mammals were responsible, at least in part, for creation of "bare zones" in grassland around *Artemisia* shrubs in southern California. The maximum number of livestock probably occurred about 1862 for cattle and 1876 for sheep. Therefore the maximum impacts of livestock grazing on the grassland came after many introduced species had arrived and made permanent places in the grassland vegetation. Although large numbers of livestock may have accumulated around the missions and on Spanish land grants before 1850, grazing in the Central Valley appears to have been relatively light until the gold rush period after 1850. The Spanish numbered about 10,000 in California by the early 1800's, but they did not settle extensively in the Central Valley (Künzel 1848). Only a part of the wild herbivorous fauna has been replaced. The introduction of livestock shifted the timing of grazing. Native ruminants may have been seasonal residents of the Central Valley (McCullough 1971, Sampson and Jespersen 1963), but they repeated that residence year after year. Nevertheless, some animal exclosures do not show a recovery by perennial grasses.

Cultivation

The largest acreage was cultivated during the 1880s, preceding extensive irrigation and depending on dry-land farming procedures. Grains and forage were the principal crops. They are still grown on some of the nonirrigated foothills. As was often the case in "boom" times, many more acres were plowed for a few crops than could be sustained in crop production. Many foothill hectares that now show little evidence of plowing, and that support annual grassland, once grew a wide variety of crops and, before that, supported perennial grasslands. Cultivation has contributed to the replacement of the pristine grassland with annuals.

Fire in the Pristine Grassland

The frequency of fires set by lightning today very likely approximates past occurrences. Although burning in pristine grassland cannot be quantified as to intensity and frequency, fire must have spread through the abundant, dry fuel, probably to a greater extent than it does today. The California Division of Forestry reported 312 lightning fires per year in its protection area, which is 43% woodland–grass. The evidence is deductive, but the conclusion is generally accepted that lightning-caused fires have been part of the entire evolutionary history of the grassland (Heady 1972).

Permanent settlements of Indians occurred along the streams and California coast during the last 8000 yr (Heizer and Whipple 1971) and perhaps longer. Early narrative reports about California mention fires set by Indians, many of which probably burned larger areas than intended (Sampson 1944). Burning by mankind came late in the evolution of the grassland species, however, and probably exerted only minor influences on the grassland.

Summary Comments

No single factor caused the demise of the pristine perennial grassland. Except for hectares in cultivation, roads, housing, and so on, the grassland boundaries probably are much the same today as they were 200 yr ago. Brush plants may have invaded in some places, but these probably balance the size of area where grassland increased after brush and woodland were removed by fire and herbicides. More likely, increase in brush density and cover after effective fire control resulted in thickened stands of woody plants rather than their invasion into new areas.

The pristine grassland received considerable but unknown impact from native grazing animals. Livestock replaced that pressure to a greater degree than it added a new impact. Rodents still remain in the grassland and perhaps occur as abundantly as they did during prelivestock times (Fitch 1948; Fitch and Bentley 1949). Droughts reduce the vigor of perennial grasses and the quantity of herbage. That, in turn, causes grazing pressures to be severe. This cyclic pressure of overgrazing in dry times and undergrazing in wet periods occurred with the wild animals before domestic animals arrived. It continues today; deer, for example, periodically overgraze their savanna type winter range on the foothills surrounding the Central Valley. Many herds of wild animals around the world fluctuate in numbers in concert with abundant or scanty forage resulting from weather cycles. I see no reason to doubt that these impacts occurred on the pristine valley grassland, that the perennial grassland occasionally received heavy use, and that livestock altered and increased grazing but did not add a completely new factor.

Into this situation came the introduced annuals, which were widely adapted to the Mediterranean climate and to the local soil, which were resistant to grazing, and which offered high competition to the perennials (Evans and Young 1972). Their passage through the dry summers in the seed stage enhanced their advantage over the perennials, especially during dry years. Evidence exists that some of the grass-

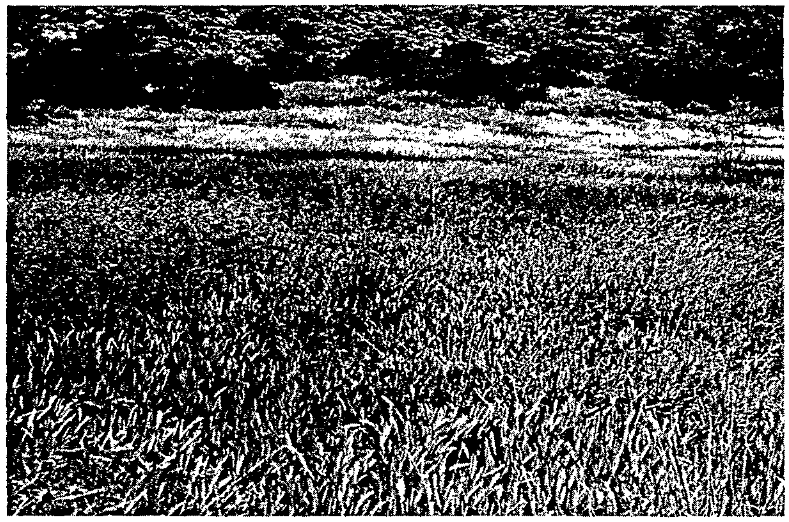

Figure 14-4. Perennial grassland dominated by *Stipa pulchra* behind and annuals in the foreground. La Jolla Valley, near Oxnard.

land became dominated by *Avena* before heavy grazing by domestic livestock occurred. Cultivation and other types of soil disturbance completely removed the perennials from many areas. The introduced annuals returned quickly after the abandonment of cultivation and held the land, preventing return of the perennials. Many factors contributed to the replacement of the perennials with introduced annuals, not the least being the competitive ability of the annuals under varying conditions of weather and grazing (Harris 1967). Replacement of the perennial grassland resulted, not from a single cause or a sequence, but from several causes operating together.

Complete absence of livestock is about the only situation that sometimes permits the reinvasion of perennial grasses. No livestock means no grazing by any large animals, as herds of elk and pronghorn antelope no longer exist. Removal of all livestock now may be as disruptive to pristine conditions as the presence of too many livestock (Heady 1968). Whether the perennial grasses will return on *all* ungrazed sites remain a question. Other than *Poa scabrella,* few perennial grass species can be found after 40 yr without grazing in the livestock-free area on the San Joaquin Experimental Range. Scattered plants and small stands of several perennial species developed in 10–15 yr without livestock grazing on the Hopland Field Station. *Stipa pulchra* cannot be found in areas with abundant annual grasses on Hastings Reservation, although it does occur in oak woodland. The stands of *S. pulchra* in La Jolla Valley near Oxnard remained after many decades of various kinds of use and have invaded the former cultivated fields and pastures in the valley center (Fig. 14-4; Barry 1972). *Stipa pulchra* abundantly appeared in one pasture on the Hopland Field Station after restriction of sheep grazing to the winter season. It decreased in the same pasture after spring, summer, and fall grazing a few years later.

Determination of the characteristics of the pristine valley grassland must not overshadow concern for the present and the future. Grassland ecologists should recognize that species labeled as "introduced" and "alien" cannot be removed and perhaps not even reduced from their present state. For example, *Bromus mollis* and *Avena fatua* usually increase when heavy grazing is reduced. They dominate on numerous soil types and over large areas. Regardless of whether managerial concerns consider them desirable or undesirable, they cannot be eliminated under any known rangeland management practice. Cultivation may remove them from the center of the field, but they remain at the edges. Ecologists and others should recognize these as "new natives".

The rest of this chapter takes that view. In accordance with these ideas, the present valley grassland system of organisms and abiotic factors will be described within the theory that the annual grassland exhibits its own location variations, vegetational changes, and responses to abiotic factors, and that it becomes relatively stable or climax if given a chance. The rationale for these views has been developed elsewhere (Heady 1975).

THE ANNUAL GRASSLAND

The term "California annual type" describes the present valley grassland. The boundaries show little change from those of the pristine perennial grassland. In other words, annual grasslands exist below 1200 m in elevation west of the Sierra Nevada–Cascade Mts. and in coastal southern California; they are best developed as a treeless ring that borders the cultivated Central Valley; they provide an understory to a *Quercus douglasii* savanna (Fig. 14-5) and in the oak woodland. Removal of the woodland and much of the chaparral results in a new or thickened stand of the herbaceous annuals until the woody plants return. The type has many variants, including climax characteristics in some areas and successional status to woody vegetation in others.

The annual vegetation contains many species. Janes (1969) encountered 124 species during the sampling of 20 sites along a transect between Kern and Humboldt

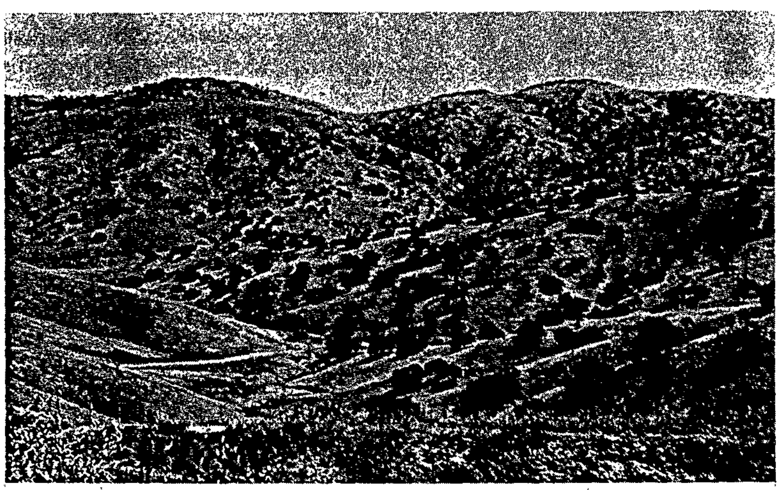

Figure 14-5. *Quercus douglasii*-annual grassland savanna.

Cos. About 50 species were recorded year after year in sampling a 625 m^2 plot on the Hopland Field Station by Heady (1956a). White (1966) found 55 species in North Field, Hastings Reservation.

Native versus Introduced Species

Robbins (1940) reported 526 species of alien plants growing without cultivation in California. Most of them are associated with cultivated and pasture lands and hence with the annual grassland. Of the species on Robbins' list, 111 were Gramineae and 96 Compositae. About 72% of the total number originated in Europe and western Asia. Of the 478 species of grasses in California, 175 were introduced and 156 are annual (Crampton 1974).

The number of species on a statewide basis tells little about the grassland. The proportion of native species in lists for individual stands varies from 71% at Hastings Reservation (White 1967) to less than 20% at Hopland (Heady 1956a) and perhaps more. Talbot et al. (1939) reported that annuals constituted 94% of the herbaceous cover in grassland, 98% in woodland, and 93% in chaparral. The introduced species constituting that cover accounted for 63%, 66%, and 54%, respectively, of the total cover. A number of studies have shown that the 6–10 most important species (various sampling methods) in the annual grassland are new natives (White 1966; Heady 1958; Talbot et al. 1939; Bentley and Talbot 1951). Bentley and Talbot (1948) reported that native annuals on the San Joaquin Experimental Range composed 20–60% of the cover, depending on rainfall pattern. The California annual grassland is a relatively new mixture of annual grasses and broad-leaved plants. Although many annual species occurred in the grassland of 200 yr ago, they are not the annuals that dominate today.

Dominants on Different Sites

Obviously, the annual grassland differs from place to place. McNaughton (1968) showed that the structure of the annual grassland varied greatly within small distances. Janes (1969) selected 20 sites at about 80 km intervals along a transect from the southern end of the San Joaquin Valley to southern Humboldt Co. Criteria for site selection included no evidence of grazing and fire for 3 yr, a minimum soil depth of 45 cm, a southerly aspect, and slope no greater than 35%. The gradient of average rainfall along the transect was 13–204 cm, as measured at the station nearest each site. In terms of foliage cover, *Bromus mollis, B. rigidus,* and *Erodium botrys,* in that order, were the principal species occurring with more than 20 cm of rainfall. *B. rigidus* reached highest proportions near 50 cm of rainfall. On 8 of the 20 sites *B. mollis* dominated the vegetation. *Bromus rubens* and *Erodium cicutarium* dominated on sites with less than 19 cm of rainfall and were found in measurable quantities to approximately 30 cm. *Avena fatua* occurred at midrange, 20–63 cm, and *A. barbata* peaked at 87–100 cm. Plots in the middle rainfall range, where *A. fatua* occured, had the highest total foliage cover and biomass per unit area. Although much variation occurs locally and from year to year, these data on botanical composition appear to represent reasonable generalitites about the distribution of the important annual species in relation to climate. Soils at the sites varied in texture between clay and gravely loams.

The California annual grassland includes a wide mixture of species, growing on many different habitats, and divisible into subtypes, depending on the purposes of the investigation. Subtypes may be designated according to soil types, as listed by Barry (1972); mapped, as in the State Cooperative Soil–Vegetation Survey (Zinke 1962); described as range sites (Bentley and Talbot 1951); or separated as objects of study for managerial purposes (Evans et al. 1975). The annual grassland responds to site variation where local differences may be controlled by soil nutrients (McGown and Williams 1968), broad north–south differences in temperature and moisture, or in allelopathic antagonisms. The leachate from straw of *Avena fatua* may reduce stands of *Centaurea melitensis* and *Silybum marianum*, thereby increasing the dominance of *A. fatua* (Tinnin and Muller 1971, 1972). Detailed analyses substantiating these general conditions exist for only a few locations. However, site-by-site data on the species composition of the grassland have been gathered for range condition evaluations by the Soil Conservation Service and for basic information by the State Cooperative Soil–Vegetation Survey (U.S. Forest Service 1954; University of California 1959).

Vegetational Changes

Phenology. The annual plants begin to germinate in the fall with the first rains exceeding about 15 mm, grow slowly through the winter, grow rapidly in the spring, and mature between late April and June. The proportion of different species varies to such an extent that grasses may dominate in some years and *Erodium* in others, and legumes may or may not be conspicuous. Several types of changes in the annual grassland have been described and quantified on the Hopland Field Station (Heady 1961) and the San Joaquin Experimental Range (Bentley and Talbot 1951; Biswell 1956). For detailed information, the reader should consult the review by McKell (1974) of autecological studies on germination, growth, flowering, and maturation of several annual grassland species.

The period of rapid spring growth brings on a progression of different dominant species. *Agoseris heterophylla, Baeria chrysostoma, Hypochoeris glabra, Lotus* spp., *Orthocarpus* spp., *Trifolium* spp., etc., flower and mature early, at about the same time. Among the grasses, *Aira caryophyllea* and *Briza minor* set seed early, *Festuca* spp. later, and *Bromus mollis* and *B. rigidus* still later. *Avena barbata* and *Erodium* spp. flower and seed throughout the spring. Early- and late-summer species include *Aristida oligantha, Eremocarpus setigerus, Gastridium ventricosum, Madia* spp., and *Taeniatherum asperum* (= *Elymus caput-medusae*).

Few descriptions of the annual grassland mention seed numbers and seed characteristics, yet most of the vegetation lives through the dry season in the seed stage. The soil seed bank makes an excellent starting point for a study of seed population dynamics. The range of numbers of seeds appears to be from about 300 (Sumner and Love 1961) to nearly 150,000 per square meter (Heady 1956b). Four other papers give numbers between 7500 and 60,000 per square meter (Batzli and Pitelka 1970; Heady and Torell 1959; Major et al. 1960; Major and Pyott 1966). Major et al. (1960) found that seeds of *Taeniatherum asperum* could be as numerous as 60,000 per square meter.

Buried viable seeds may live for several years. Major and Pyott (1966) found a poor correspondence between seed numbers and the vegetation above the seed bank.

Obviously, not all the species that can occur in the vegetation over a period of years will be evident at any one time. After extensive review of the literature on field germination in annual grassland, Bartolome (1976) concluded that the relationship between soil seed available (single species or *in toto*) at the beginning of the season and later vegetational patterns has not been quantitatively established. Numerous laboratory studies have been made on the characteristics of seed germination and seedling establishment of species in the annual grassland. Data concerning differential seed and seedling mortality in the field no not exist for the first few days or weeks of the growing season.

A 2 yr study of seedling establishment and plant numbers on the Hopland Field Station by Bartolome (1976) showed that near-maximum seedling densities for most species occurred before the second week of the growing season. However, seedlings of *Aira caryophyllea, Briza minor,* and *Hypochoeris glabra* appeared in the winter and spring. *Eremocarpus setigerus,* a summer-active species, germinated in the spring. Plant densities differed between the 2 yr, but total standing crop (biomass) did not. Soil seed numbers far exceeded seedling numbers in most species, suggesting that environmental factors exert more influence on plant densities than does seed supply.

Mulch, or above-ground plant residue, influences germination and seedling establishment through modification of several microenvironmental factors. Most seeds germinate on the soil surface or at depths to 1 cm below it. Seedlings must become established in a critical zone, which is the top few centimeters of soil and the lower 3–5 cm of atmosphere. Mulch on the soil surface results in physical conditions that favor microorganisms, seedlings, water infiltration, rapid decomposition, and other factors. More precise understanding of soil surface processes and relationships is needed. The lack of field data on germination, seedling establishment, dynamics of seed numbers, dynamics of seedling establishment, seed production, and seed dormancy is surprising in view of a widespread belief that the botanical composition of the annual grassland stems from patterns of seed numbers, germination, and seeding establishment.

By clipping a new set of replicates every 2 wk between October 15 and May 30, the normal growth patterns of eight annual species became clear (Savelle and Heady 1970). All plants were grown in the same soil and under the same conditions of watering and ambient temperatures. The period of maximum growth rate ranged from early March to early May (Fig. 14-6). Flower initiation began in early February in *Erodium botrys* but did not start until April in *Festuca megalura.* No two of the species studied were alike in growth pattern. Under drying spring weather in field conditions, rapid growth rates may show an abrupt ending.

Significant changes occur in numbers of plants and biomass per unit area as the season progresses. Biswell and Graham (1956) reported more than 20 seedlings per square centimeter after germination, but it is more likely that the average approximates 3–5 per square centimeter (Heady 1958). Both papers reported 10–90% mortality during the growing season, depending on species. The relative densities of *Bromus mollis* and *B. rigidus* tended to increase during the growing season, whereas those of shorter plants decreased. A study near Berkeley by Ratliff and Heady (1962) determined that several species reached their individual maximum biomass on the following dates in 1960: *Bromus mollis* on April 24, *Erodium cicutarium* on April 30, *Medicago hispida* on May 8, *Bromus rigidus* on May 21, *Avena fatua* on

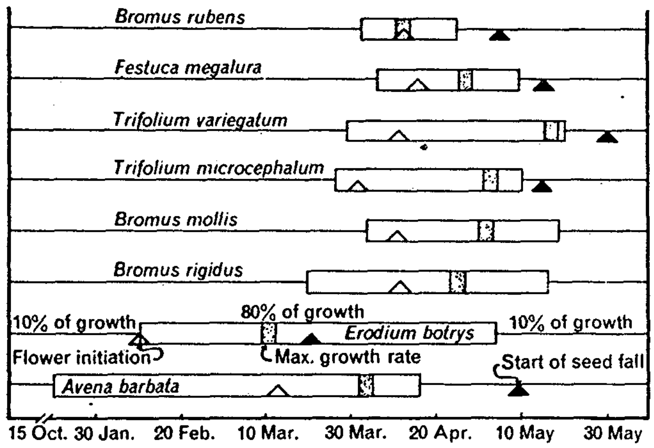

Figure 14-6. Time periods and approximate dates of growth, flower initiation, and seed fall for eight common annual species grown in pots under uniform soil, regular watering, and ambient temperatures. (Savelle and Heady 1970).

May 21, and *Lolium multiflorum* on May 28. The biomass for the whole community peaked on May 21. Two weeks later, 23% of the above-ground weight had been lost through shattering and seed fall. Broad-leaved species tended to disappear rapidly after plant maturity. In 1 wk, 79% of the *Erodium* biomass disappeared. A 19 yr study at Hopland by Heady (see Pitt 1975) showed that the March 1 biomass averaged 90 g m^{-2}, and the June 1 biomass 309 g m^{-2}. Year-to-year variation halved and doubled these averages.

Three sets of data on biomass, productivity, botanical composition, and weather have been analyzed by Murphy (1970) for the purposes of developing predictive relationships on the Hopland Field Station. He found that precipitation in November correlated (r^2 = 0.7) with forage yield several months later. Duncan and Woodmansee (1975) used 24 yr of data on the San Joaquin Experimental Range to find that peak forage yields were only poorly correlated with precipitation in any particular month or with annual precipitation. Pitt (1975), using Heady's data from Hopland Field Station, also obtained poor relationships between yield and precipitation alone. The inclusion of temperatures and periods without precipitation improved the regressions and explained more of the variation. If germination occurs early in the fall, production will be high, but periodic spring precipitation without dry soil between showers until May is also needed for greatest biomass yield (Hooper and Heady 1970).

The weight of herbage biomass at the end of the growing season differs severalfold among years. Duncan and Reppert (1960) reported a production range of 775–2,900 kg ha^{-1} over a 25 yr period on the San Joaquin Experimental Range. During the winter until about the first of March, green herbage might be scarce in some years and abundant in others. Above-ground standing crop on March 1 varied between 24 and 218 g m^{-2}, but high March weights were not always followed by high June weights (Pitt 1975).

Overseeding of a set of plots on the Hopland Field Station resulted in one plot having a high proportion of *Medicago hispida* in 1957 and the adjacent plot being relatively high in *Bromus mollis*. The following year, with no treatments and no grazing, both plots had high *Bromus* composition and no *Medicago*. These differences show the great and overriding impact of annual weather patterns on the annual grassland. An early fall rain followed by a long dry period results in large amounts of *Erodium botrys*. Grasses require continuous rainfall, or at least dry periods no longer than 2–3 wk.

Successional changes in the annual grassland. In 1951, Sampson et al. described successional trends in the annual grassland due to differences in grazing pressure. Under reasonable grazing management, tall species such as *Avena fatua* and *Bromus mollis* dominate, but with heavy grazing shorter species prevail. Close grazing delays fall growth and reduces winter growth (Talbot and Biswell 1942; Bentley and Talbot 1951). A study of the effects of natural plant residue on the composition and production of annual vegetation suggests that increasing the degree of herbage removal results in less biomass production and fewer floristic changes. With no mulch at the time of germination, *Aira carophyllea, Baeria chrysostoma, Hypochoeris glabra,* and *Orthocarpus erianthus* dominated the vegetation on plots in Mendocino Co. (Heady 1956a). Different but similarly short, broad-leaved species occupied plots with no mulch in other parts of the annual grassland (Heady, unpub. data). Ratliff et al. (1972) found that *Eschscholzia californica* var. *peninsularis, Festuca megalura, Orthocarpus purpurascens,* and *Trifolium* spp. had high frequencies in stubble fields. *Bromus rigidus* and *Erodium botrys* dominated in old fields. When plant residue was left on the ground in a plot at Hopland, *Bromus mollis* increased from 0.9% to 37.3% of the cover in 3 yr. When all the mulch was removed each year, the proportion of *B. mollis* continued at less than 2% (Heady 1965). Many other authors have recognized the importance of natural mulch in the maintenance of the annual grassland (Talbot and Biswell 1942; Hedrick 1948; Hervey 1949; Biswell 1956). Apparently mulch alters botanical composition through influence on physical conditions at the soil surface and on the bulk density of the surface soil horizon. Mulch has little influence on pH and phosphorus and nitrogen contents in the grassland system (Table 14-1).

General observations suggest that fields of forbs, especially in early to middle spring, indicate early successional stages, while dominance by grasses may be climax annual grassland (Fig. 14-7). With due regard for vegetational alterations caused by site, weather pattern, and other factors, a number of species are placed in successional position in Table 14-2. This list must be interpreted with care and altered to fit local areas. For example, *Bromus rubens* and *Erodium cicutarium* are middle successional or even lower on areas with annual precipitation greater than 25 cm or after removal of chaparral. *Erodium botrys* may characterize all the successional stages and fluctuate in abundance more in concert with seasonal rainfall patterns than with successional factors. The alphabetical arrangement in the list in Table 14-2 implies that relative importance cannot be assigned throughout the annual grassland. However, this list reflects a widely held view that succession exists among the wide spectrum of annual species. Native perennial grass species become part of the climax, but they will not completely replace the annuals.

Genetic changes in the annual species. Quantitative studies in the interplay of immigration, migration, and natural selection are insufficient to permit evaluation

TABLE 14-1. Average herbage production for 1954-60, and average total nitrogen, total phosphorus, and bulk density in the top 7.6 cm of soil in 1960 after 8 yr of mulch manipulation. Treatment 1 had all mulch removed, Treatment 8 had none removed, and the other treatments represented an intermediate scale of mulch removal (Heady 1965)

Mulch Treatment	Herbage ($g\ m^{-2}$)	Total Nitrogen ($kg\ ha^{-1}$)	Total Phosphorus ($kg\ ha^{-1}$)	Soil Bulk Density ($g\ cc^{-1}$)
1	115	1242	224	1.36
2	168	1547	245	1.30
3	196	1425	225	1.25
4	199	1478	226	1.21
5	204	1410	229	1.26
6	225	1623	249	1.26
7	232	1555	231	1.23
8	254	1524	232	1.14

of genetic and evolutionary changes in the annual grassland. Presumably the relatively small gene pool within a new arrival and the wide range of habitats available to the immigrants could have stimulated speciation. Jain et al. (1970) found that *Bromus mollis* was genetically variable but had not shown as much geographical differentiation as had other species. Knowles (1943) did distinguish a coastal and an inland strain of *B. mollis*, based on time from germination to flowering. Marshall and Jain (1969) showed that the genetic systems in *Avena barbata* and *A. fatua* may be important determinants of the relative population sizes in mixed stands. Stebbins (1965) described many of the annuals as weeds with wide adaptive ranges, so a few migrant individuals could quickly adapt to many habitats. McKell et al. (1962) claimed that probably a single introduction of *Taeniatherum asperum* evolved over 70 yr into a number of genotypes differing in morphological and physiological characteristics. These and other authors have used species in the annual grassland to study breeding systems of species, groups of species, and genetic principles, but little is known about the impact of genetic changes and speciation on the grassland vegetation.

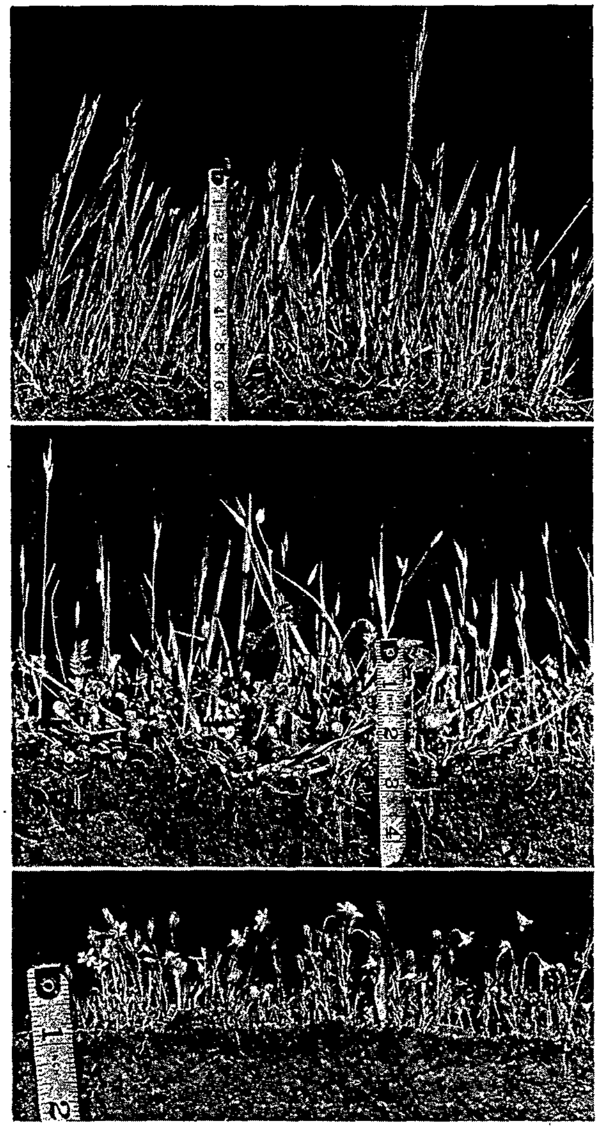

Figure 14-7. Natural grassland on 2.5 cm thick strips of soil illustrating plant successional stages. Top: climax dominated by *Bromus rigidus* and *Bromus mollis*. Center: Intermediate stage dominated by *Medicago hispida* and *Erodium botrys*. Bottom: Early successional stage with abundant *Baeria chrysostoma.*

Annual Grassland Responses to Grazing

With reasonable intensities of grazing by livestock, no soil erodes, productivity of biomass ramains high, and floristic composition of the vegetation shows little change. In fact, annual grassland withstands remarkably heavy livestock use (Bentley and Talbot 1951; Heady 1961). Stocking rates 2–3× normal for a year or more do more economic damage to the livestock operation than permanent biological damage to the landscape. However, moderate season-long or year-long grazing is recommended.

Animals spread over the range take the most palatable forage and leave the coarse materials as plant residue. The residue serves to protect new seedlings and promote water infiltration into the soil, and it fosters a low soil bulk density. Heady (1965) has shown that approximately 500 kg ha^{-1} of above-ground plant residue at the beginning of the rainy season indicates proper intensity of grazing use. This standard applies at approximately 75–100 cm of rainfall. Criteria for areas with more and less rainfall have not been determined. Light grazing results in abundant tall grasses, and heavy grazing sets the succession back to low-growing plants, but unless continued indefinitely, overgrazing has short-term effects.

Annual Grassland Responses to Fire

Burning in the grassland probably diminished after the discovery of gold because increased plowing and overgrazing reduced the amounts of fuel. However, settlers, stockmen, and lumbermen burned the forest and chaparral types to convert them to grasslands.

Fires in the grassland have little permanent effect. Few seeds are destroyed by grassland fires (Bentley and Fenner 1958). Species composition sometimes changes toward more broad-leaved plants and fewer annual grasses (Hervey 1949). Burning apparently does not alter moisture content, temperature, and organic matter in soil where grazing has already removed most of the above-ground biomass. Cook (1959) documented a reduction in rodent numbers due to fire, but all species survived.

TABLE 14-2. Plants usually found in climax, middle, and low successional stages. N = native species

Climax	Middle in Succession	Low in Succession
Avena barbata	Daucus pusillus (N)	Aira caryophyllea
A. fatua	Erodium botrys	Briza minor
Bromus mollis	Festuca dertonensis	Eremocarpus setigerus (N)
B. rigidus	F. megalura	Hordeum hystrix
B. rubens	F. myuros	Madia spp.
Erodium cicutarium	Gastridium ventricosum	Lupinus bicolor (N)
Taeniatherum asperum	Medicago hispida	Trifolium spp. (N)

Many of the effects of burning duplicate those of mulch removal by hand (Talbot et al. 1939; Heady 1956a) and none of the changes has been detected beyond the third year after burning. Charred organic materials, in contrast to the white ash that follows intensive fires, leave the surface black and provide a soil cover.

Attempts to control *Taeniatherum asperum,* a late-maturing species, with prescribed fire have been abandoned. A fire in dry grass when the *Taeniatherum* seed is immature destroys many seeds, but enough escape to produce the next crop.

SUBJECTS FOR RESEARCH

A marjority of the research papers on the ecology of the valley grassland originated from studies at the San Joaquin Experimental Range, the Hopland Field Station, and the campuses of the University of California at Berkeley, Davis, and Santa Barbara. These papers place more emphasis on management than on basic ecological processes. Therefore subjects with minimal immediate practical application dominate my list of research suggestions.

1. With further study, the spatial variation of grassland species in relation to climate would be better understood.
2. Very little is known about the rates of organic matter accumulation and decomposition in grassland.
3. The taxonomy and population dynamics of decomposers need attention.
4. Experiments into the competition between annual and perennial herbaceous plants would help to define the new climax valley grassland.
5. The relative impacts of many kinds of grazing animals remain almost unknown.
6. Seed population dynamics in relation to grazing and climate needs more work.
7. The tule marshes and saltbush variations of this type have not been mapped, described, or studied in either their original or their present conditions.
8. On the practical side, measurement of pollution impacts on valley grassland would help to define the future of much land in the Central Valley of California.

LITERATURE CITED

Adams, A., and J. Muir. 1948. Yosemite and the Sierra Nevada. Houghton Mifflin, Boston. 130 p.

Barry, W. J. 1972. The Central Valley prairie. Calif. Dept. Parks and Recreation, Sacramento. 82 p.

Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. Science 170:1210-1212.

Bartolome, J. W. 1976. Germination and establishment of plants in California annual grassland. Ph.D. dissertation, Univ. Calif., Berkeley.

Batzli, G. O., and F. A. Pitelka. 1970. Influence of meadow mouse populations on California grassland. Ecology 51:1027-1039.

Beetle, A. A. 1947. Distribution of the native grasses of California. Hilgardia 17:309-357.

Bentley, J. R., and R. L. Fenner. 1958. Soil temperatures during burning related to postfire seedbeds on woodland range. J. For. 56:737-740.

Bentley, J. R., and M. W. Talbot. 1948. Annual-plant vegetation of the California foothills as related to range management. Ecology 29:72-79.

-----. 1951. Efficient use of annual plants on cattle ranges in the California foothills. USDA Circ. 870. 52 p.

Biswell, H. H. 1956. Ecology of California grassland. J. Range Manage. 9:19-24.

Biswell, H. H., and C. A. Graham. 1956. Plant counts and seed production on California annual-type ranges. J. Range Mange. 9:116-118.

Burcham, L. T. 1956. Historical backgrounds of range land use in California. J. Range Manage. 9:81-86.

-----. 1957. California range land. Calif. Forestry, Sacramento. 261 p.

Burtt-Davy, J. 1902. Stock ranges of northwestern California. USDA Bur. Plant Ind. Bull. 12. 81 p.

Clements, F. E. 1934. The relict method in dynamic ecology. J. Ecol. 22:39-68.

Cook, S. F., Jr. 1959. The effect of fire on a population of small rodents. Ecology 40:102-108.

Crampton, B. 1974. Grasses in California. Calif. Nat. Hist. Guide 33. Univ. Calif. Press, Berkeley, Calif.

Duncan, D. A., and J. N. Reppert. 1960. A record drought in the foothills. USDA Forest Serv., Pac. SW Forest and Range Exp. Sta. Misc. Paper 46. 6 p.

Duncan, D. A., and R. G. Woodmansee. 1975. Forecasting forage yield from precipitation in California's annual rangeland. J. Range Manage. 28:327-329.

Evans, R. A., B. L. Kay, and J. A. Young. 1975. Microenvironment of a dynamic annual community in relation to range improvement. Hilgardia 43:79-102.

Evans, R. A., and J. A. Young. 1972. Competition within the grass community, pp. 230-246. In V. B. Younger and C. M. McKell (eds.). The biology and utilization of grasses. Academic Press, New York.

Fitch, H. S. 1948. Ecology of the California ground squirrel on grazing lands. Amer. Midl. Natur. 39:513-596.

Fitch, H. S., and J. R. Bentley. 1949. Use of California annual-plant forage by range rodents. Ecology 30:306-321.

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

Harris, G. 1967. Some competitive relationships between Agropyron spicatum and Bromus tectorum. Ecol. Monogr. 37:89-111.

Heady, H. F. 1956a. Changes in a California annual plant community induced by manipulation of natural mulch. Ecology 37:798-812.

-----. 1956b. Evaluation and measurement of the California annual type. J. Range Manage. 9:25-27.

-----. 1958. Vegetational changes in the California annual type. Ecology 39:402-416.

-----. 1961. Continuous vs. specialized grazing systems: a review and application to the California annual type. J. Range Manage. 14:182-193.

-----. 1965. The influence of mulch on herbage production in an annual grassland. Proc. 9th Internat. Grassland Congr. 1:391-394.

-----. 1968. Grassland response to changing animal species. J. Soil Water Conserv. 23:173-176.

-----. 1972. Burning and the grasslands in California. Proc. Ann. Tall Timbers Fire Ecol. Conf. 12:97-107.

-----. 1975. Structure and function of climax, pp. 73-80. In Proc. Third Workshop of the U.S./Austral. Rangelands Panel. Soc. for Range Manage.

Heady, H. F. and D. T. Torell. 1959. Forage preferences exhibited by sheep with esophageal fistulas. J. Range Manage. 12:28-34.

Hedrick, D. W. 1948. The mulch layer of California annual ranges. J. Range Manage. 1:22-25.

Heizer, R. F., and M. A. Whipple. 1971. The California Indians: a source book. Univ. Calif. Press, Berkeley. 619 p.

Hendry, G. W. 1931. The adobe brick as a historical source. Agric. Hist. 5:110-127.

Hervey, D. F. 1949. Reaction of a California annual-plant community to fire. J. Range Manage. 2:116-121.

Hooper, J. F., and H. F. Heady. 1970. An economic analysis of optimum rates of grazing in the California annual-type grassland. J. Range Manage. 23:307-311.

Jain, S. K., D. R. Marshall, and K. Wu. 1970. Genetic variability in natural populations of soft chess (Bromus mollis L.). Evolution 24:649-659.

Janes, E. B. 1969. Botanical composition and productivity in the California annual grassland in relation to rainfall. M.S. thesis, Univ. Calif., Berkeley. 47 p.

Knowles, P. F. 1943. Improving an annual brome grass, Bromus mollis L., for range purposes. J. Amer. Soc. Agron. 35:584-594.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Spec. Pub. 36.

Kunzel, H. 1848. Upper California (transl. from German by Anthony and Max Knight). Book Club of Calif., San Francisco, 1967.

Lin, J. W. Y. 1970. Floristics and plant succession in vernal pools. M.S. thesis, San Francisco State Univ. 99 p.

Luckenbach, R. 1973. Pogogyne, polliwogs, and puddles - the ecology of California's vernal pools. Fremontia 1(1):9-13.

Major, J., C. M. McKell, and L. J. Berry. 1960. Improvement of Medusahead infested rangelands. Calif. Agric. Exp. Sta. Leafl. 123. 3 p.

Major, J., and W. T. Pyott. 1966. Buried viable seeds in two California bunchgrass sites and their bearing on definition of a flora. Vegetatio 13:253-282.

Marshall, D. R., and S. K. Jain. 1969. Interference in pure and mixed populations of Avena fatua and A. barbata. J. Ecol. 57: 251-270.

McCullough, D. 1971. The tule elk. Univ. Calif. Press, Berkeley. 209 p.

McGown, R. L., and W. A. Williams. 1968. Competition for nutrients and light between the annual grassland species Bromus mollis and Erodium botrys. Ecology 49:981-990.

McKell, C. M. 1974. Morphogenesis and management of annual range plants in the United States, pp. 111-123. In K. W. Kreitlow and R. H. Hart (eds.). Plant morphogenesis as the basis for scientific management of range resources. USDA Misc. Pub. 1271.

McKell, C. M., J. P. Robinson, and J. Major. 1962. Ecotypic variation in medusahead, an introduced annual grass. Ecology 43:686-698.

McNaughton, S. J. 1968. Structure and function in California grasslands. Ecology 49:962-972.

Munz, P. A., and D. D. Keck. 1959. A California flora. Univ. Calif. Press, Berkeley. 1681 p.

Murphy, A. H. 1970. Predicted forage yield based on fall precipitation in California annual grasslands. J. Range Manage. 23:363-365.

Perkins, J. E. 1864. Sheep husbandry in California, pp. 134-145. In Trans. Calif. State Agric. Soc. 1863.

Pitt, M. D. 1975. The effects of site, season, weather patterns, grazing, and brush conversion on annual vegetation, Watershed II, Hopland Field Station. Ph.D. dissertation, Univ. Calif., Berkeley. 281 p.

Ratliff, R. D., and H. F. Heady. 1962. Seasonal changes in herbage weight in an annual grass community. J. Range Manage. 15:146-169.

Ratliff, R. D., S. E. Westfall, and R. W. Roberts. 1972. More California poppy in stubble field than in old field. USDA Forest Serv. Res. Note PSW-271. 4 p.

Robbins, W. W. 1940. Alien plants growing without cultivation in California. Calif. Agric. Exp. Sta. Bull. 637. 128 p.

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

Sampson, A. W., A. Chase, and D. W. Hedrick. 1951. California grasslands and range forage grasses. Calif. Agric. Exp. Sta. Bull. 724. 130 p.

Sampson, A. W., and B. S. Jesperson. 1963. California range brushlands and browse plants. Univ. Calif. Agric. Exp. Sta. Manual 33. 162 p.

Savelle, G. D., and H. F. Heady. 1970. Mediterranean annual species: their response to defoliation, pp. 548-551. In Proc. 11th Internat. Grassland Cong.

Shantz, H. L., and R. Zon. 1924. Atlas of American agriculture. Section E: Natural vegetation. USDA Bur. Agric. Econ. 29 p.

Stebbins, G. L. 1965. Colonizing species of the native California flora, pp. 173-191. In H. G. Baker and G. L. Stebbins (eds.). The genetics of colonizing species. Academic Press, New York.

Stebbins, G. L., and J. Major. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35:1-35.

Sumner, D. C., and R. M. Love. 1961. Resident range cover often cause of seeding failures. Calif. Agric. 15(2):6.

Talbot, M. W., and H. H. Biswell. 1942. The forage crop and its management, pp. 13-49. In C. B. Hutchison and E. I. Kotok (eds.). The San Joaquin Experimental Range Calif. Agric. Exp. Sta. Bull. 663.

Talbot, M. W., H. H. Biswell, and A. L. Hormay. 1939. Fluctuations in the annual vegetation of California. Ecology 20:394-402.

Tinnin, R. O., and C. H. Muller. 1971. The allelopathic potential of Avena fatua: influence on herb distribution. Bull. Torrey Bot. Club 98:243-250.

-----. 1972. The allelopathic influence of Avenu fatua: the allelopathic mechanism. Bull. Torrey Bot. Club 99:287-292.

Twisselmann, E. C. 1967. A flora of Kern County, Calif. Wasmann J. Biol. 25(1-2):1-395.

U. S. Forest Service, Pacific Southwest Forest and Range Experiment Station. 1954. Field manual, soil-vegetation surveys in California. 95 p.

University of California Department of Agronomy. 1959. Field manual, grassland sampling. Supplement No. 1 to Field manual, Soil-Vegetation Survey. 14 p.

White, K. L. 1966. Old-field succession on Hastings Reservation, California. Ecology 47:865-868.

-----. 1967. Native bunchgrass (Stipa pulchra) on Hastings Reservation, California. Ecology 48:949-955.

Zinke, P. J. 1962. The soil-vegetation survey as a means of classifying land for multiple-use forestry. Proc. 5th World For. Congr. 1:542-546.

CHAP

1

ROBERT H
SUBODH J

Department o
University of C