No poet has yet sung the full beauty of our poppy, no painter has successfully portrayed the satiny sheen of it lustrous petals, no scientist has satisfactorily diagnosed the vagaries of its variations and adaptability. In its abundance, this colorful plant should not be slighted: cherish it and be ever thankful that so rare a plant is common.

—John Thomas Howell (1937)

California is historically and metaphorically symbolized as the "Golden State" in tribute to the gold rush of 1849, but for many living in the state gold is also a reminder of its sunny Mediterranean climate, or perhaps the Golden Gate Bridge. The 'Washington' navel orange was "liquid gold" from which fabulous wealth was created in the late nineteenth century.

The coastal plains and valleys were also once golden with fields of brilliant wildflowers, highlighted by the stunning California poppy (Eschscholzia californica), as well as goldfields (Lasthenia spp.) that created bright vellow rugs. California hillsides also hosted a rainbow of other colors from tidy tips, fiddlenecks, lupines, phacelias, owls clover, baby blue eyes, penstemon, and many other genera. The splendor of California native wildflowers was early disseminated to many parts of the known world by word of mouth and in the writings of those first explorers who cruised along the California coast and saw long stretches of rolling hills clothed in a mantle of gold. The first Spanish galleons sailing up and down the coast in the eighteenth century called the region "a land of fire," noting the deep orange-colored hillsides of California poppies. Their spontaneous exclamation, "la tierra del fuego!" (the land of fire) became a symbol of this rich, newfound land. California's wildflower heritage was appreciated by the generations of the late nineteenth century, was the topic of books (e.g., Holder 1889; Saunders 1914, 1931), was institutionalized in floral societies, and was the primary inspiration of the New Year's Day Rose Parade in Pasadena (the Tournament of Roses). Indeed, the

poppy was chosen as the state flower by the State Floral Society, an effort passed by legislation in 1903.²

In modern times, California's "gold" is advertised in tabletop books that show glossy photographs of yellow oak-dotted rolling hillsides. While the trees are native, the yellow undercarpet is an assemblage of bromes, oats, fescues, barleys, and mustards introduced to California from Mediterranean Europe and the Middle East. Over the past two centuries, European annual species have proliferated across the state, a process that began with the deliberate introduction of some of these invaders by Spanish Franciscan missionaries in 1769. This treasure deemed "golden" is in fact a biological transformation, but naïve Californians are oblivious to the immense change in annual herbaceous vegetation. Invasive grasses and forbs have diminished the diversity and abundance of the state's wildflower flora, degraded pasture, and have increased fuels that threaten urban areas with wildfire. The tragedy is that the poppy, California's state flower, is no longer common, to the point that reserves have recently been created to protect it.

Perhaps the most remarkable aspect of California's biological invasions is their furious pace, as herbaceous cover had already changed over extensive areas of the state before the arrival of the first botanists to California in the early nineteenth century, a topic of many scientific investigations (e.g., Mooney and Drake 1986; Bartolome et al. 1986; Huenneke 1989; Keelev 1989, 1993; Bossard et al. 2000). The rapid change in herbaceous vegetation has hampered investigation to a point that the pre-European herbaceous flora is enigmatic to most scholars in the modern scientific community (Barry 1972; Bartolome at al. 1986; Keeley 1989; Hamilton 1997; Mack 1989), leading to a plethora of hypotheses about the indigenous flora and time line and mechanisms of the transformation. The modern consensus is that California was carpeted not by wildflowers, but by perennial bunch grassland that became replaced by modern exotic annual grassland, encouraged by grazing and drought in the mid-nineteenth century (reviewed in Heady 1977; Keeley 1989, 1993; Sims and Risser 2000). This view appears to originate with the observations of William Henry Brewer, who led the first survey of the state's flora in the 1860s (Brewer and Watson 1876–80). The prominent early twentieth century ecologist Fredrick Clements (1934) formally proposed the bunch grassland model, which he deduced using his climax and "relict" theories. Modern grassland specialists have undertaken ecological and restoration studies on bunch grasslands (e.g., Nelson and Allen 1993; Dyer and Rice 1997; Hamilton et al. 1999).

Advocates of the bunch grassland theory write with certainty. Referring to purple needle grass, Heady (1977: 495) writes, "Stipa (Nassella) pulchra, beyond all doubt, dominated the valley grassland. . . . Perennial grasses associated with Stipa were Aristida hamulosa (ternipes), Elymus glaucus, E. triticoides, Festuca idahoensis, Koeleria cristata, Melica californica, M. imperfecta, and Poa scrabella (secunda)." Burcham (1957: 90), referring to the pre-Hispanic landscape, writes that "the pristine dominants were perennial bunchgrasses—purple needle grass (Stipa pulchra) and nodding needlegrass (Stipa [Nassella] cernua) [and] were outstanding in the Central Valley. Blue wild-rye, pine blue grass, and deergrass were important associates" (cf. Beetle 1947). In North American Terrestrial Vegetation, Sims and Risser (2000: 342) state that the "original Pacific prairie was dominated by cool-season, perennial bunchgrasses such as Nassella pulchra, N. cernua, Elymus spp., and Poa secunda."

Annual and perennial wildflowers were important components of the bunchgrass prairie (Barbour et al. 1993). Burcham (1957: 104) states that "associated with the grasses, . . . were . . . broad-leaved herbs with brightly colored flowers." Early studies describe "great masses of annuals" comprising several hundred species and more than 50 genera (Clements 1920, 1934; Weaver and Clements 1938; Jepson 1925; Beetle 1947; Barbour et al. 1993). In "A California Flora," Munz and Keck (1959: 18) describes a "subtropical type" of open treeless grassland, with a "rich display of flowers in wet springs." Still other botanists and ecologists assert that bunch grasslands were never a prominent component of the state's vegetation (Twisselmann 1967; Wester 1981; Hamilton 1997; Schiffman 2000).

A second theme is whether human disturbance was critical to the expansion of introduced annual grasses and forbs. Until the late nineteenth century, the novel source of disturbance in California was the introduction of domestic livestock, largely cattle, but also horses for tending cattle and sheep. An important question is whether the expansion of introduced species was largely facilitated by livestock or was pushed ahead, dispersing and colonizing based on the introduced species' ecological requirements, seed-dispersal capacity, and other life traits. As stated by Blumler (1995), a major issue is the extent to which anthropogenic disturbance is necessary for alien species' invasions. On one hand species may have been ruderal, strongly dependent on disturbance for success, while other species may have transplanted vigorous adaptations from one continent to another, outcompeting native species.

Advocates of the bunch grass hypothesis argue that perennial grassland was replaced by introduced annual forbs and introduced grasses pri-

marily during early American settlement in the mid-nineteenth century due to overgrazing (Burcham 1957; Barry 1972; Keeley 1989). According to Burcham (1957: 192), a leading proponent, "With reservoirs of seed of aggressive annuals widely distributed about the countryside . . . recurrent [droughts] . . . combined with extremely heavy grazing during the late 1850s and 1860s, struck the final blow at the once abundant perennial grasses of the range lands. . . . As perennials were depleted the burden of grazing fell upon the more palatable of the native and introduced annuals." The linkage between expanding exotics and displacement of bunch grasses was even made in top-flight botanical floras, used by botanists for decades. For example, in A California Flora, Munz and Keck (1959: 17) describe "Valley grassland" as "originally being covered with various bunch grasses such as Stipa (Nassella) pulchra, S. cernua, Poa scabrella (secunda) and Aristida divericata; now because of overgrazing largely replaced by annual species of Bromus, Festuca, Avena, etc."

This view may even have deeper roots. Livestock grazing at scales of millenia in Europe selected for weedy, aggressive annuals that expanded across California (Zohary 1962, 1973; Baker and Stebbins 1965; Sauer 1988; cf. Blumler 1995 and Blumler and Byrne 1991). A corollary argument is that lightly grazed California pasture was vulnerable to invasion from grazing-adapted Mediterranean annuals (Mack and Thompson 1982), i.e., native California annuals were noncompetitive against introduced species because they evolved without grazing pressure.

Another hypothesis is that exotic species expanded across California independently of human disturbance, i.e., they determined their own destinies as invasive species (Mooney and Drake 1986; Huenneke and Mooney 1989; D'Antonio and Vitousek 1992; Blumler 1995; Bossard et al. 2000; Brooks et al. 2004). Introduced species were "preadapted" in California wildlands because they came from similar climates in the Mediterranean basin, invading almost exclusively preexisting herbaceous landscapes (Heady 1977; Huenneke 1989). The invaders were also highly productive, thereby using resources more efficiently than indigenous forbs (Huenneke 1989; Blumler 1995), even strongly competing against native perennials (Biswell 1956; McNaughton 1968; Heady 1977; Bartolome and Gemmill 1981; D'Antonio and Vitousek 1992; Blumler 1995). Introduced Mediterranean annuals also came to California without their natural pathogens (Jackson 1985). Scholars have further pointed out that not all of California was invaded at once, as exotic species came at different times and spread at different rates into divergent habitats depending on their life traits (Heady 1977; Sauer 1988).

As bunchgrass theory has come under scrutiny, some researchers have

posited another theory that annual forbs dominated California's prairies (Biswell 1956; Bartolome and Gemmill 1981; Wester 1981; Hamilton 1997; Schiffman 2000). Accounts of scarce plant cover in the Central Valley suggest that bunch grasses were not present in these areas and that vivid descriptions of wildflowers were made throughout California (Wester 1981). The remarkable success of exotic annual grasses and forbs cannot be denied. Modern exotic annual grasslands have extensive distribution on clay-rich soils and alluvium at lower elevations throughout California, including on the coastal plains and in interior valleys of central and southern California and inland across the Central Valley to the foothills of the Sierra Nevada (Figure 1.1) (Heady 1977; Sims and Risser 2000). Exotic annual grasslands are free of woody cover over extensive areas or grow beneath oak woodlands in the mountains and foothills. Exotic annual grassland reaches its limit where it interfaces with coastal sage scrub and chaparral on shallow, poorly developed soils on well-drained slopes of the Sierra Nevada, the central Coast Ranges, and the Transverse and Peninsular Ranges of southern California. California grasslands grow in a wide range of average annual precipitation, which mostly falls between November and April, ranging from 20 to 100 centimeters. Thin cover of exotic annual grassland even extends into the desert on the leeward side of the Sierra Nevada and southern California ranges. The dominant species of exotic annual grassland include Bromus madritensis (rubens), B. diandrus, Avena fatua, A. barbata, Brassica nigra, B. geniculata, Hordeum murinum, and Festuca megalura (myuros) (Heady 1977). Annuals forbs are diverse, but scarce, and include annual species in the genera Eschscholzia, Phacelia, Cryptantha, Salvia, Nemophila, Viola, Chaenactis, Lavia, and perennials such as Allium and Nassella (Raven 1963; Ornduff 2003). The growing season is the winter rainy season, when temperatures are warm enough to maintain growth flushes and hard frosts are rare (Minnich 2006). Exotic and native annuals germinate soon after the first heavy rains, grow slowly in winter, and then grow rapidly to flower and seed in spring. Drying when soil moisture is depleted is followed by fires if there is sufficient growth from winter rains. The seed of natives and exotic forbs may survive for years to decades as soil "seed banks," whereas exotic grasses have short seed life of a year or two, but compensate through massive germination rates with the first rains.

While there is unanimous agreement in the scientific community that herbaceous vegetation has undergone enormous change since the late eighteenth century, little consensus has emerged on the nature of the transformation largely because existing hypotheses have limited empirical foundation. Thus far, the web of models and hypotheses on the history



Figure 1.1. Generalized distribution of exotic annual grassland in California (mapped from MODIS Rapid Response System, http://rapidfire.sci.gsfc.nasa.gov).

of California's herbaceous flora has little direction toward synthesis. For reasons of practicality, nearly all ecological research is based on local field studies covering a few years, which precludes the generation of realistic null hypotheses (Jackson et al. 2001). Studies have also resorted to deductive historical scenarios based on spatial evidence, often in relation to the modern population dynamics of already invasive-contaminated

herbaceous ecosystems. Without historical perspective and baselines from which vegetation change can be reconstructed, the conclusions drawn may be ad hoc stories.

The goal of this volume is to assess pre-European herbaceous vegetation and its transformation to modern exotic grasslands. The approach here follows the perspective of Grove and Rackham (2001: 18), who assert that "landscape history is best arrived at from the records of identifiable sites which can be traced down the centuries." Hypotheses concerning biological invasions in California's herbaceous communities can be best "tested" by examining historical records of introduced species, native vegetation, and grazing of sufficient time scale to capture vegetation change.

The choice of baseline to reconstruct historical vegetation change also affects the outcome, a phenomenon that Jackson et al. (2001) call the "shifting baseline syndrome." Defenders of the bunch grassland model have built their case on historical evidence from the mid-nineteenth century, based on a longstanding view that only observations by trained botanists have scientific merit (Parish 1920; Burcham 1957). However, the first botanists saw already widespread grasslands of introduced European annual grasses and forbs. This book begins with the earliest historical baseline, the journals kept by Spanish missionary explorers during the Gaspar de Portolá and Juan Bautista de Anza land expeditions in the late eighteenth century. These documents are the only written record of indigenous herbaceous cover before invasive species began spreading across California. The Spanish account may possibly capture California's herbaceous vegetation at Holocene time scales. Until the arrival of the Spaniards, long-range seed dispersal was near background rates at geologic time scales because Native American hunting and gathering societies, the population in California possibly numbering 350,000 (Baumhoff 1963), were limited in mobility, precluding accelerated the anthropogenic dispersal of seed plants seen in recent centuries.

While Spanish botany is not at the level of modern scientific protocol, the journals of the Portolá, Anza, and other Spanish expeditions are a systematic survey of the state as required by mandate of the viceroy of Mexico, and they provide a baseline of aboriginal vegetation against which one can assess changes in California's vegetation. Moreover the recent publication of the original diaries of Juan Crespí (Brown 2001) has brought greater detail concerning California vegetation at the onset of European settlement. The Crespí diaries translated by Bolton (1927) were scribe copies that generalized the original manuscripts. To make effective use of the Spanish diaries requires two concessions from the reader: (1) the broadscale pattern does not require that the diaries be highly pre-

cise (Jackson et al. 2001); and (2) the diaries should be appreciated as originating from the mind-set of late-eighteenth century Spanish priests (Grove and Rackham 2001).

Indigenous forbfields similar to those described by the Spaniards were the object of discussion in the nineteenth and early twentieth centuries by botanists, naturalists, explorers, and book writers devoted to California's diverse landscapes, and in articles of the same localities in the *Los Angeles Times* well into the twentieth century. These sources and writings of explorers, naturalists, and settlers in the post-Hispanic era vividly capture the arrival and expansion of some European grasses and forbs, and related impacts such as the displacement of wildflowers and the proliferation of wildfires in the deserts.

This book evaluates the regions settled or explored during the Spanish mission period: California south of San Francisco and west of the Sierra Nevada, as well as the southeastern deserts (Figure 1.1). The following questions will be addressed: (1) the character of pre-European herbaceous vegetation; (2) patterns of aboriginal burning; (3) the expansion of introduced species and displacement of native herbaceous vegetation; and (4) where, when, and how many domestic livestock grazed, and what was the role of grazing in the transformation of California pasture.

The hope is that this study will encourage new studies and models of California's herbaceous vegetation that conform to the historical record. The central hypotheses of this book are the following: (1) California's pre-Hispanic vegetation consisted of vast carpets of wildflowers, not bunch grasslands; (2) the introduction of European species triggered a biological invasion without the help of man's activities such as grazing; (3) the transformation of herbaceous cover began along the coast and shifted inland, the pace of change being dependent on habitat, climate variability, and, most importantly, the time of arrival and adaptive modes of the invaders; and (4) the collapse of indigenous forblands over most of California happened right in front of our eyes with the invasion of bromes in the twentieth century.