

FOURTEEN

Valley Grassland

JAMES W. BARTOLOME, W. JAMES BARRY, TOM GRIGGS, AND
PETER HOPKINSON

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Several names have been applied to the low-elevation grasslands that lie west of the Sierra-Cascade crest and, in southern California and Baja, California, west of the Northern Peninsular Ranges (Fig. 14.1). Clements (1934) famously called single-species stands along railway rights-of-way in

the Central Valley the "*Stipa pulchra* consociation of the California bunch grass prairie." Numerous authors later refer to the area simply as the "California prairie" or the "California annual grassland." The first name emphasizes the supposedly perennial nature of the original grassland taxa, and the latter draws attention to the current dominance of annual plants.

Burcham (1957) and Munz (1959) described the California prairie as valley grassland with southern affinities and a coastal prairie with northern relationships. Küchler (1964) labeled these communities California steppe and *Festuca-Danthonia* grassland, respectively. This chapter concentrates on the valley grassland of Mediterranean climates termed the California Ecological Province by Barry and Foster (1997). Chapter 7 discusses the coastal prairie, which is part of the Pacific Northwest Ecological Province.

Most of the present-day valley grassland that lies below 1,200 m is dominated by annual plants (Heady 1977). The California annual grassland is therefore largely synonymous with valley grassland. It is most simply described as a treeless belt that borders the cultivated Central Valley. In addition, many of the same annual species provide an understory to *Quercus douglasii* savanna and oak woodland (Allen-Diaz et al. 1999). Küchler's (1964) map shows that 5.35 million ha support valley grassland, and an additional 3.87 million ha have an oak overstory (Heady).

Climate is the primary controlling factor in the valley grassland, severely constraining most management and restoration activities (Jackson and Bartolome 2002). California's Mediterranean climate is characterized by cool, wet winters and hot, dry summers. Average annual rainfall for valley grassland ranges from about 12 cm in the southwestern San Joaquin Valley to 200 cm in northwestern California. Importantly, rainfall amount and timing vary enormously from year to year, the variation following no predictable trend (Heady et al. 1991). Regardless of annual

[MB6] FIGURE 14.1 Distributional limits of the "Valley Grassland" vegetation type. Note that it extends to the coast along the central and southern parts of California.



rainfall, soil water deficits characterize the grassland ecosystem for 4 to 8 summer months every year (Heady 1977).

Valley grassland is an unusual vegetation type in that it comprises largely nonnative, naturalized grass and forb species that are annuals, in contrast to the putative original grassland dominants, perennial bunchgrasses (Heady 1956b). In many areas of the grassland, native species form only a small percentage of the herbaceous cover (Biswell 1956; Heady et al. 1991; Hamilton, Griffin, and Stromberg 2002), although native species remain rich in number of taxa, and their cumulative cover even makes them dominants in a few areas. Possibly driven by overgrazing and drought in the late 1800s, or simply by the introduction of highly competitive, Mediterranean grassland species adapted to the Californian climate, type-conversion from the original valley grassland to the annual grassland was nearly total, and many rangeland ecologists view it as irreversible (Heady 1977; Heady et al. 1991). However, the increasing success of native species restoration on some sites has tempered that view (see Conservation and Restoration Issues).

Valley grassland is species-rich. Commonly, >50 species are found in 30 × 30 m plots (Heady et al. 1991). Nonnative, annual species contribute heavily to this species richness, however (Heady 1956b). The dominant species are all nonnative. *Bromus hordeaceus* and two *Erodium* species are most characteristically dominant: *E. botrys* in wetter areas

and *E. cicutarium* in drier areas, often in association with introduced *Vulpia* species. *B. diandrus* is very common, although generally in low numbers, and *B. madritensis* ssp. *rubens* is dominant on many dry sites. *Avena barbata*, *A. fatua*, and *Lolium multiflorum* can dominate locally (Tinnin and Muller 1971), but they generally are not as widespread in the grassland as the other dominant species unless livestock use is light or absent (Heady et al.).

Valley grassland includes plant associations that exhibit enormous spatial and temporal variability, notably from site to site within the growing season, and from year to year on the same site (Heady 1958; Sawyer and Keeler-Wolf 1995). Species composition and biomass production vary spatially in relation to distance from the coast (Burcham 1975), average annual precipitation (Janes 1969; Bartolome, Stroud, and Heady 1980), elevation (Burcham 1975), and slope and aspect (Evans, Kay, and Young 1975). Additional variation on smaller spatial scales, including soil type and presence of a woody overstory, has often been observed (Burcham 1957; Holland 1973; McClaran and Bartolome 1989).

Valley grassland also exhibits huge temporal variation. Biomass changes dramatically over the course of a single growing season. Although germination follows fall rains, cool winters allow little growth. Only in spring do warm temperatures stimulate rapid growth and flowering. Following seed-set from April to June, cool-season annuals are rep-

[MB1]

resented only in the seed bank until the fall. A few warm-season annuals reach their peak growth during the summer. Year-to-year fluctuations in rainfall timing and amount and in temperature greatly influence interannual differences in species composition and biomass production. Directional change occurs over the long term, as new species and diseases successfully invade, fire and grazing regimes are altered, and the global climate changes.

Recently, Jackson and Bartolome (2002) have proposed adding a third subtype, the Coast Range grassland, to the traditionally bipartite classification of California's grasslands (valley grassland and coastal prairie). Transitional between the two types, the Coast Range Grassland shares the mesic coastal climate of coastal prairie, but unlike the latter, grasses and forbs of valley grassland and sports limited perennial grass cover. Distinctive species of the Coast Range grassland include *Erodium botrys*, *Vulpia*, and *Bromus hordeaceus*; annual *Trifolium* species are also common. Because the Coast Range grassland species composition is similar to that of the Valley Grassland and as yet little researched, we treat both types here.

Well-known reviews of valley grassland include Heady's (1977), with a later, brief update (1988, 1012–1013), Huenneke and Mooney (1989), and Heady et al. (1991).

Relation to Other Vegetation Types

The Palouse prairie, centered in eastern Washington and Oregon, is related to the Valley Grassland because of closely similar climates, floras, and growth habitats of the dominants. The Palouse prairie lies in the rain shadow of the Cascades and has a generally semiarid climate, similar to that of the Valley Grassland; yet the Palouse historically resembled the mixed-grass vegetation of the Great Plains grasslands, except for the absence of short grasses (Heady 1977). Perennial grasses such as *Festuca idahoensis*, *Koeleria macrantha*, *Poa secunda* ssp. *secunda*, *Leymus condensatus*, and *Elymus elymoides* occur 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 Valley Grassland. The Palouse dominant, *Pseudoroegneria spicata*, and the presumed California zonal dominant, *Nassella pulchra*, are not shared (Beetle 1947). In addition, Stebbins and Major (1965) found, from genetic and paleobotanical evidence, that many endemic species of the Valley Grassland originated from northern ancestors.

Nassella pulchra stands dominate coastal terrace grasslands south of Morro Bay and transition into the Coastal Prairie northward to Salt Point where stands are confined to south-facing slopes. Here, the mesic to wet coastal prairie is dominated by *Deschampsia cespitosa* ssp. *holciformis*, and stands of *D. cespitosa* occur as far south as San Simeon State Park and the high elevations of Tuolumne Meadows, Yosemite National Park, and as far eastward as Mono Lake Tufa State Reserve in the Great Basin. *Danthonia californica* stands of the Coastal Prairie extend south along the coast to San Simeon State Park.



FIGURE 14.2 Valley grassland dominated by *Avena barbata* after 50 years of livestock exclusion.

A transition between valley grassland and Mojave Desert steppes occurs over a short distance on the eastern slopes of the Tehachapi and other southern California mountains. For example, *Nassella cernua* and *Achnatherum speciosa* replace *N. pulchra* and *Leymus triticoides* of the valley grassland. A similar transition occurs from the Peninsular Ranges into the Sonoran Desert. Valley grassland taxa, such as *Achnatherum coronatum* and *Distichlis spicata*, extend into the Sonoran Desert.

Valley grassland extends into the understory of oak savannas and woodlands, as well as into chaparral and other scrub vegetation types with little change in its herbaceous characteristics (Fig. 14.2). Large specimens of *Quercus lobata* may be found in the Great Central Valley and smaller valleys in the Coast Ranges and Transverse Ranges; often *Elymus glaucus* dominates in the drip line. In some cases, *Leymus condensatus* dominates the understory, especially in the Transverse Ranges. The gentle beginning slopes of the mountains bordering the Great Central Valley are covered with Valley Grassland, but *Quercus douglasii* gives the grassland a savanna aspect. Here, *E. glaucus*, and in more moist soils *Koeleria macrantha*, dominates the *Quercus* understory. Burcham (1957) suggested that the savanna appearance covered more area in primeval times than it does today.

The northern coastal scrub dominant, the short-lived shrub *Baccharis pilularis*, invades and modifies grassland, often quite far inland (Hobbs and Mooney 1986; Williams, Hobbs, and Hamburg 1987). Using a chronosequence of remote images, Russell and McBride (2003) documented a conversion of grassland to *B. pilularis*-dominated coastal scrub in five of seven sites in the San Francisco Bay Area.

Sharp boundaries between grassland and chaparral are usual (Fig. 14.3). Davis and Mooney (1985) showed that early season and surface soil water use by the grasses, their limited seed dispersal, and herbivory within and adjacent to the chaparral, combined with plant-water relations within the adjacent bare zone could explain the observed, stable plant distributions.

Poorly drained alkali soils occur most abundantly in the southern and western sides of the San Joaquin Valley, and the Carrizo Plain, which lack oceanic drainage. Bordering bare soil within the sinks, alkali-tolerant species such as



FIGURE 14.3 Boundary between chaparral and valley grassland/oak woodland caused by soil differences, Mt. Diablo, Contra Costa County.

Allenrolfea occidentalis, *Kochia californica*, *Salicornia subterminalis*, and *Suaeda fruticosa* occur. Grasses, such as *Distichlis spicata*, *Hordeum depressum*, and *Sporobolus airoides*, characterize the wet alkali grasslands. With somewhat better drainage and on foothill areas, *Atriplex polycarpa* dominates, and the annual grassland species appear as an understory (Twisselmann 1967). A small area of *Artemisia tridentata* is also present in the southern inner Coast Ranges. Inner coastal hills in San Benito County support *Atriplex polycarpa*, *Ephedra californica*, and *Pyrrocoma 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," mainly along the eastern side of the Central Valley, are small depressions that fill with fresh water during the rainy season. An endemic flora has evolved in these vernal pools with the surrounding mima mounds supporting more regional grassland taxa.

On the global scale, valley grassland has a climate and flora similar in many respects to those of the world's other Mediterranean regions: southern Europe (Jackson 1985), the Middle East (Naveh 1967), Chile (Gulmon 1977; Arroyo et al. 1995), and Australia. Leiva, Chapin, and Fernandez Ales (1997) compared the grassland of Spain with that of California. Peco and her colleagues (Espigares and Peco 1993; Peco and Espigares 1994; Peco, Ortega, and Levassor 1998; Peco et al. 2003) have documented many similarities in savanna structure and function between Spain and California.

The Original California Grassland

Judging from the present distribution of numerous perennial grass species, the original grassland was extensive (Beetle 1947) and corresponded roughly with the extent of the present annual grassland. Exceptions may be areas taken for cultivation and urban development and Southern California sites that were formerly shrublands (Keeley 1990). Other exceptions include soils with most of the A horizon eroded

away that now support scrub or chaparral, and oak stands cut for charcoal or firewood that now support grasslands.

The ecosystem dynamics of the original California grassland are unknown; even the species composition is uncertain. Reports before 1900 by explorers, survey parties, and botanical collectors provide some information about the kinds of plants in California's grasslands, but these limited vegetational descriptions give only a glimpse of an already altered landscape (Heady 1977; Barbour 1996). Studies of tree rings, pollen, phytoliths, and archeological sites give clues to the nature of these grasslands prior to the influence of Eurasians, as well as prior to American Indian settlement.

Edwards (1992, 1996) believes that the Valley Grassland evolved under heavy seasonal grazing regimes during the Pleistocene. Needlegrasses are presumed to have evolved from isolated steppe progenitors as the Mediterranean-type climate slowly developed over the past 5 million years. This evolution did not include the development of tolerance to constant, heavy grazing pressure, characteristic of steppes and prairies in other parts of the world. At least through the Holocene Epoch, large grazing animals may not have been as numerous a component of the Valley Grassland as in comparable grassland ecosystems (Robinson 1968).

During the late Pleistocene (18,000 BP), temperate open woodland and savanna vegetation of *Juniperus*, *Artemisia*, and *Sarcobatus* appears to have dominated the California grassland landscape. This vegetation was similar to that currently extant in parts of the Great Basin, with a steppe understory of *Aristida*, *Deschampsia*, *Elymus*, *Festuca*, *Leymus*, and *Pseudoroegneria*. Much of the Pleistocene megafauna was associated with this pristine vegetation. The extinction of the Pleistocene megafauna occurred during the dramatic climatic changes of the early Holocene: Edwards (1992, 1996) puts this date at around 10,000 years BP. Of the 18 late-Pleistocene grazing and/or browsing mammals found in central California, only 3 survived the Holocene: elk, deer, and pronghorn.

The new Holocene grassland communities were formed with fewer large grazing mammals and an ever-increasing human presence. Table 14.1 lists typical vertebrates of the postglacial grasslands (Shelford 1963; Storer 1965; Heady 1968). The Holocene grasslands were mainly grazed by tule elk and antelope, as well as by deer, rabbits, and numerous rodents. California Indians hunted these animals, possibly intensively enough to have kept their populations down. Tule elk ranged throughout the great Central Valley, migrating up into adjacent foothills in winter when flooding occurred and in late summer when vegetation was dry.

The California tule elk population is estimated to have numbered 500,000 at Eurasian contact (Lockwood 2004), and California grasslands likely supported several million pronghorn. Pronghorn were originally very abundant in the San Joaquin Valley, as in other bunchgrass areas, occurring in herds of 2,000 to 3,000. They fed largely on grasses, only occasionally on twigs and leaves of shrubs. The Beechey ground squirrel (*Spermophilus beecheyi*) was one of the most characteristic taxa of the Valley Grassland. Because this

TABLE 14.1

Typical Vertebrates of the Postglacial Grasslands

Pronghorn	<i>Antilocapra americana</i>
Tule elk	<i>Cervus elaphus nanmodes</i>
Deer	<i>Odocoileus hemionus</i>
Coyote	<i>Canis latrans</i>
Grizzly bear	<i>Ursus arctos</i>
Black-tailed jackrabbit	<i>Lepus californicus</i>
Ground squirrel	<i>Ammospermophilus and Spermophilus species</i>
California vole	<i>Microtus californicus</i>
Badger	<i>Taxidea taxus</i>
Botta's pocket gopher	<i>Thomomys bottae</i>
San Joaquin pocket mouse	<i>Perognathus inornatus</i>
Western meadowlark	<i>Sturnella neglecta</i>
Horned lark	<i>Otocoris alpestris</i>
Brewer's blackbird	<i>Euphagus cyanocephalus</i>
Desert sparrow hawk	<i>Falco sparveriusphalaena</i>
Horned owl	<i>Bubo virginianus</i>
Pacific rattlesnake	<i>Crotalus viridis</i>
Gopher snake	<i>Pituophis melanoleucus</i>

[MB5] From Shelford (1963), Storer (1965), and Heady (1968).

species increases with heavy grazing (Bartolome 1997), it may have been much less abundant than today. The impact of insect herbivores on California's original grassland (and present-day grassland) is little understood (Joern 1989).

It is thought that during the late Holocene, *Nassella pulchra* was the principal taxon throughout the Great Central Valley but not along the coast (Oosting 1956; Heady et al. 1991). According to Clements and Shelford (1939), *Elymus glaucus*, *Poa secunda* ssp. *secunda*, and *Muhlenbergia rigens* were important associates in the needlegrass community. Only one of the dominant grasses in this community departs from the bunchgrass habit: *Leymus triticoides*, a sod-former. This grass formed extensive stands in the central portion of the San Joaquin Valley, as well as in some of the larger coastal valleys. In the southern Coast Ranges and southern California, *N. lepida* and *Achnatherum parishii* shared the role of principal dominants with the two interior taxa. Important associated grasses were *Koeleria macrantha*, *Melica imperfecta*, *Muhlenbergia rigens*, and various *Aristida* (Burcham 1957). *E. glaucus* was characteristic of the oak savanna, whereas *N. lepida* and *Achnatherum coronatum* were common on upper slopes along the valley grassland-California chaparral ecotone, in the chaparral, and in the oak savanna (Burcham 1957; Shelford 1963).

In 1977, Heady (495) unconditionally stated, "[*Nassella pulchra*, beyond all doubt, dominated the valley grassland."

However, shortly thereafter, challenges to the theory of perennial grass dominance arose (see Hamilton 1997 for a thorough deconstruction of the perennial bunchgrass paradigm), arguing for annual forb-dominated types (Wester 1981; Blumler 1992, 1993, 1995; Schiffman 2000; Holstein 2001), shrub-dominated types (Keeley 1990, 2002; Hopkinson and Huntsinger 2005), and rhizomatous graminoid-dominated types (Holstein), depending on region. Little direct evidence of perennial dominance exists. 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 (Heady). Some direct evidence for bunchgrass domination was suggested by phytolith (a plant microfossil) analysis at Jepson Prairie, Solano County (Bartolome, Klukkert, and Barry 1986).

The frequency of fires set by lightning today very likely approximates past occurrences. Although burning in the original grassland cannot be quantified as to area 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).

For more than 10,000 years, an estimated population of 200,000–400,000 California Indians lived in the riparian forests, woodlands, savannas, prairies, steppes, and grassland barrens of the California Ecological Province. California Indians used fire extensively—after seed harvest to renew grasslands, to drive and trap wild grazing animals, to produce goods, to control insects and disease, as well as to prosecute warfare (Keeley 2002). Historical accounts leave no doubt that Indian-set fires were common in grassland ecosystems as well as in associated shrub lands, savannas, woodlands, and forest lands. This practice dates back at least 5,000 years and was not confined to the Valley Grassland but included all but desert regions of California. Coastal terraces, prairie balds, mima mounds, riparian zones, wetlands, montane meadows, as well as savanna, woodland, and forest understories were all under frequent, low-intensity fire cycles. Lightning as an ignition source was more common on higher ridges but also occurred in lower elevations, though usually at a different time of year. Thus, the Valley Grassland evolved with a fire-return interval possibly as short as 1–3 years, with an annual fire cycle of spring to autumn burns (Barry 2003). These burns were set after harvesting grass seeds and were differential; that is, California Indians burned the more xeric south slopes, knolls, and ridges first, then more mesic sites such as valley floors and north-facing slopes, and last wet sites once they had dried and been harvested (Barry).

Putatively remnant perennial communities of valley grassland are mainly dominated by two perennial bunchgrasses: *Nassella pulchra* and *N. cernua*. Stands of *N. pulchra*

currently exist from Valle de Las Palmas, Baja, California, and from San Diego County northward to Salt Point State Park in Sonoma County (mainly on coastal terraces and valleys). Toward the southern end of the grassland, *N. cernua* increases in importance. Perennial grasses associated with *Nassella* include: *Festuca idahoensis*, *Koeleria macrantha*, *Melica californica*, *M. imperfecta*, *Aristida ternipes* var. *hamulosa*, and *Poa secunda* ssp. *secunda*. Annual grasses included *A. oligantha*, *Deschampsia danthonioides*, *Vulpia microstachys* var. *pauciflora*, and *Orcuttia*. Broad-leaved forbs include many perennials, especially plants with bulbs, and annuals in the Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Fabaceae, and Lamiaceae (Stebbins 1965).

Bunchgrasses are liberally supplemented by erect grasses such as *Bromus carinatus* and by a few stoloniferous perennials and are interspersed with numerous annuals, primarily native forbs and nonnative grasses. These communities are best represented on xeric to mesic ultramaphic edaphotopes to which alien Mediterranean annual grasses are not well adapted. Wet ultramaphic edaphotopes often contain solid stands of *Muhlenbergia rigens*. Most wet edaphotopes are dominated by the stoloniferous *Leymus triticoides*, which often forms extensive stands, whereas *Sporobolus airoides* dominates wet alkaline edaphotopes. Alkali flats support stands of the stoloniferous *Distichlis spicata*. Needlegrass prairie communities gradate into xeric bunchgrass steppe communities in the San Joaquin Valley as soil moisture declines; here, *Poa secunda* ssp. *secunda* or, occasionally, *Aristida hamulosa* predominate. According to Ernest Twisselmann (pers. comm.), steppe communities are replaced with native annual grassland communities wherever annual rainfall is below 21 cm. *Vulpia microstachys* var. *pauciflora* is the most frequent annual grass of these desert grasslands (Barry 2003).

Replacement of the Original Grassland

With the Eurasian occupation of California came plant introductions from all over the world: some intentional, some accidental. Nonnative grasses and forbs such as *Poa annua*, *Hordeum murinum*, *Lolium multiflorum*, and *Erodium cicutarium* made almost immediate headway into California as evidenced by adobe-brick and pollen studies (Hendry 1931; Heady et al. 1991; Mensing and Byrne 1998). Taxa from environments that are similar but have separate evolutionary histories and dissimilar floras (southern Europe, Chile, southwest Australia, and South Africa) have successfully invaded the California grassland and have mixed with the original vegetation of California (Baker 1989). These regions with Mediterranean climates now share many species (Leiva, Chapin, and Fernandez Ales 1997).

One of the main factors which shifted the competitive advantage from native to nonnative grasses appears to be the inability of native grasses to compete successfully under heavy, year-round grazing conditions. The use of the California grasslands for domestic livestock dates from the arrival of

the first Spanish colonists in 1769, and sustained livestock grazing began around 1773 (Mason 1970). Widespread grazing in the Central Valley greatly expanded in 1824, beginning when land grants for the vast cattle ranchos were made under the Mexican Liberal Colonization Act. Once domestic grazing animals were introduced, the original bunchgrass community quickly disappeared in most of the Valley Grassland (Clark 1956). Relictual native grassland communities were usually limited to substrates such as ultramaphic soils to which non-native annuals were poorly adapted.

Tule elk, pronghorn, and many other grassland species declined precipitously. Some species, such as the Beechey ground squirrel (Bartolome 1997; Fehmi, Russo, and Bartolome 2005) and the California vole, may have increased in numbers. Joern (1989) proposed that grasshopper species might have accelerated the transformation of the original perennial grassland to annual grassland. Most grasshopper feeding in the Central Valley occurs from mid-May to late August/September, a period when annuals are only present in the seed bank, while perennials remain vulnerable to concentrated insect herbivory. Over a number of years, grasshopper herbivory may have reduced the ability of perennial grasses to compete successfully against annual species. In addition, livestock grazing may have enhanced forage quality, thus sustaining larger grasshopper populations. The homopteran *Xerophloea viridis* also fed on native grasses, but little is known about the remainder of the original invertebrate population (Shelford 1963).

California grasslands are unusual in that human manipulation was minimal until relatively recently. They were among the last of the world's temperate grasslands to be cultivated. Starting in the mid-1800s, much of the grassland was plowed. The largest acreage was cultivated during the 1880s, preceding extensive irrigation and depending on dryland farming procedures (Heady 1977). As much as 75% of the area of the Great Central Valley's central counties was converted to agriculture during this period (Huenneke 1989), grain being the major crop until early in the last century. Burcham (1957) estimated that >50% of the original California grasslands have been converted to agricultural, urban, and industrial uses. Many foothill hectares that now show little evidence of plowing, and that support annual grassland, once grew a wide variety of crops (Heady).

Fire regimes also changed over this period. Indian burning declined as Indian populations declined, to be replaced with burning by Spanish, Mexican, and United States ranchers. Starting in the early 1900s, widespread fire suppression greatly reduced Replacement of the perennial grassland resulted not from a single cause but from several factors operating together. The original grassland received considerable but unknown impact from native grazing animals. Livestock intensified that pressure (more than it added a new impact). Rodents still remain in the grassland, and some perhaps occur more abundantly than they did during pre-livestock times (Fitch 1948; Fitch and Bentley 1949; Bartolome 1997; Fehmi, Russo, and Bartolome 2005).

Droughts reduce the vigor of perennial grasses and the quantity of herbage.

Into this situation came the introduced annuals, widely adapted to Mediterranean climate and to local soil (Jackson 1985). The annuals were resistant to grazing, and they competed strongly with the perennial grasses (Evans and Young 1972). Their passage through dry summers in the seed stage increased their advantage over the perennials, especially during dry years. Cultivation and other types of soil disturbance completely removed perennials from many areas, whereas introduced annuals returned quickly after the abandonment of cultivation and held the land, preventing a return of the perennials. Many factors contributed to the replacement of the perennials with introduced annuals, not the least being the competitive ability of annuals under varying conditions of weather and grazing (Harris 1967).

Alteration of grazing and fire regimes, along with the planting of bunchgrass seedlings have sometimes produced successful reestablishment of perennial grasses in the Valley Grassland. However, removal of all livestock may be as disruptive to restoration as the presence of too many livestock because livestock exclusion can favor non-native annual species such as *Bromus diandrus* and *Avena* (Heady 1968; Heady et al. 1991). Whether perennial grasses will eventually return on all ungrazed sites and how many exotics will remain are important but still largely unanswered questions. Other than *Poa secunda* ssp. *secunda*, few perennial grass species can be found after 70 years without grazing in the livestock-free area on the San Joaquin Experimental Range (Heady 1977). Scattered plants and stands of several perennial species quickly appeared after livestock exclusion on the Hopland Research and Extension Center (REC), but succession toward native dominance was not steady, and annuals still persist after nearly 50 years (Merenlender et al. 2001). *Nassella pulchra* abundantly appeared in one pasture at Hopland REC after restriction of sheep grazing to the winter season, but it decreased in the same pasture after spring, summer, and fall grazing a few years later (Heady 1977).

The Annual Grassland

The evolution of models for grassland vegetation change began with Clementian theory (Clements 1916), which spawned a group of models best termed "equilibrium-type," emphasizing community stability and the role of biotic interactions in community development. Notably, these equilibrium models included the quantitative range condition model (Dyksterhuis 1949), which has been applied to management of California grasslands with only modest success (Sampson, Chase, and Hedrick 1951; Heady 1977; Heady et al. 1991).

In the 1950s, workers in the California annual grassland developed nonequilibrium models that emphasized the inherent dynamics of vegetation change at multiple spatial and temporal scales (Heady 1956b; Bartolome 1989a; Jackson and Bartolome 2002). Physical factors, like soil and

weather, dominate any biotic interaction, and biotic controls on productivity and composition are limited to the effects of residual dry matter (Heady 1956a; Bartolome, Stroud, and Heady 1980; Bartolome et al. 2002). Biotic interactions can still be locally important, but they must be very carefully placed in the correct spatial and temporal context, especially when summarizing and evaluating a wide variety of published reports. As suggested for rangelands in general by Westoby Walker, and Noy-Meir (1989), and confirmed for the California annual grassland by Jackson and Bartolome (2002), predicting management effects in this kind of system may require an unprecedented level of site- and time-specific information. The California annual grassland may perhaps be best understood as a mixed equilibrium/non-equilibrium system, depending on the spatial and temporal scale of interest.

The high overall species richness of the Valley Grassland tells little about this variable and complex vegetation type. A number of studies have shown that the 6 to 10 most dominant species (various sampling methods) in the annual grassland are exotics (Talbot, Biswell, and Hormay 1939; Bentley and Talbot 1951; Heady 1958; White 1966). However, the proportion of native species varies considerably from site to site, for example, 75% at Hastings Natural History Reservation (White 1967; Knops, Griffin, and Royalty 1995) but <20% at Hopland REC (Heady 1956a). Heady et al. (1991) reported that the proportion of natives on six Valley/Coast Range Grassland sites ranged from 28% to 73% and the proportion of annuals from 75 to 100% (Table 14.2). Talbot, Biswell, and Hormay. (1939) reported for the San Joaquin Valley that annuals constituted 94% of the herbaceous cover in grassland with introduced species accounting for 63% of the cover. Bentley and Talbot (1948) reported that native annuals on the San Joaquin Experimental Range composed 20% to 60% of the cover, depending on rainfall pattern. In a survey of some 40 sites of pristine grassland in the Central Valley and south coastal valleys of California, Barry (1972) found that they all contained many introduced annual species. Comparing two grassland patches in the San Francisco Bay Area, one with and one without perennial grasses, Fehmi and Bartolome (2002) found that the presence of perennials had little impact on overall community structure or on the mix of associated annuals. In eastern Contra Costa County, species composition for five annual grassland plots was 21% native and 9% perennial, whereas species composition for five nearby "relictual bunchgrass" plots was 42% native and 21% perennial; in both plot types, however, cover of non-native annuals was >85% (Bartolome et al. unpublished data; Tables 14.3 and 14.4).

Temporal Scales

California's annual grassland varies on at least three important temporal scales: intra-annual change within a single growing season, differences between years, and directional

TABLE 14.2
 Numbers of Annual and Perennial Species, both Native and Introduced, Sampled in Six Annual Grassland Sites

Site	Grassland Type	Mean Annual Rainfall (cm)	Life Form			Origin			Species Richness
			Perennial	Annual	%A	Introduced	Native	%N	
Hopland REC (Mendocino County Coast Range)	Coast Range Grassland	100	3	33	92	15	21	58	36
Jeffers Ranch (Sacramento Valley)	Coast Range Grassland	65	1	21	95	6	16	73	22
Russell Reservation (San Francisco Bay Area)	Coast Range Grassland	65	0	18	100	13	5	28	18
Panoche Hills (San Joaquin Valley)	Valley Grassland	20	0	6	100	3	3	50	6
Kettleman Hills (San Joaquin Valley)	Valley Grassland	16	1	17	94	7	11	61	18
Temblor Range (San Joaquin Valley)	Valley Grassland	20	2	6	75	4	4	50	8

NOTE: Adapted from Heady et al. (1991).

TABLE 14.3

Combined Species Composition and Percentage Relative Cover for Five Annual Grassland Plots at Vasco Caves Regional Preserve, Eastern Contra Costa County

<i>Scientific Name</i>	<i>% Relative Cover</i>	<i>Common Name</i>	<i>Origin</i>	<i>Life Form</i>	<i>Family</i>
<i>Lolium multiflorum</i>	59	Italian Rye-grass	Introduced	Annual	Poaceae
<i>Bromus hordeaceus</i>	10	Soft Brome	Introduced	Annual	Poaceae
<i>Avena fatua</i>	7	Common Wild Oats	Introduced	Annual	Poaceae
<i>Erodium botrys</i>	5	Broad-leaf Filaree	Introduced	Annual	Geraniaceae
<i>Medicago polymorpha</i>	4	Bur Clover	Introduced	Annual	Fabaceae
<i>Avena</i> sp.	2	Wild Oats	Introduced	Annual	Poaceae
<i>Vulpia bromoides</i>	2	Brome Fescue	Introduced	Annual	Poaceae
<i>Bromus diandrus</i>	2	Ripgut Brome	Introduced	Annual	Poaceae
<i>Bromus sterilis</i>	1	Sterile Brome	Introduced	Annual	Poaceae
<i>Hordeum marinum</i> ssp. <i>gussoneanum</i>	1	Mediterranean Barley	Introduced	Annual	Poaceae
<i>Bromus madritensis</i>	1	Foxtail Brome	Introduced	Annual	Poaceae
<i>Avena barbata</i>	<1	Slender Wild Oats	Introduced	Annual	Poaceae
<i>Erodium cicutarium</i>	<1	Redstem Filaree	Introduced	Annual	Geraniaceae
<i>Hordeum murinum</i> ssp. <i>leporinum</i>	<1	Foxtail Barley	Introduced	Annual	Poaceae
<i>Torilis nodosa</i>	<1	Hedge Parsley	Introduced	Annual	Apiaceae
Stone Serif Italic ssp. <i>madritensis</i>	<1	Foxtail Brome	Introduced	Annual	Poaceae
<i>Hirschfeldia incana</i>	<1	Shortpod Mustard	Introduced	Perennial	Brassicaceae
<i>Brassica nigra</i>	<1	Black Mustard	Introduced	Annual	Brassicaceae
<i>Bromus</i> sp.	<1	Brome	Introduced	Annual	Poaceae
<i>Carduus pycnocephalus</i>	<1	Italian Thistle	Introduced	Annual	Asteraceae
<i>Erodium moschatum</i>	<1	White-stemmed Filaree	Introduced	Annual	Geraniaceae
<i>Hypochaeris glabra</i>	<1	Smooth Cat's Ear	Introduced	Annual	Asteraceae
<i>Trifolium willdenovii</i>	<1	Tomcat Clover	Native	Annual	Fabaceae
<i>Triphysaria pusilla</i>	<1	Dwarf Owl's Clover	Native	Annual	Scrophulariaceae
<i>Vulpia myuros</i> var. <i>hirsuta</i>	<1	Foxtail Fescue	Introduced	Annual	Poaceae
<i>Bromus sterilis</i> / <i>madritensis</i>	<1		Introduced	Annual	Poaceae
<i>Chlorogalum</i> <i>pomeridianum</i>	<1	Soaproot	Native	Perennial	Liliaceae
<i>Lepidium nitidum</i>	<1	Shining Pepperweed	Native	Annual	Brassicaceae
<i>Microseris douglasii</i> ssp. <i>tenella</i>	<1	Douglas' Silverpuffs	Native	Annual	Asteraceae

(continued)

TABLE 14.3 (continued)

Scientific Name	% Relative Cover	Common Name	Origin	Life Form	Family
<i>Sanicula bipinnata</i>	<1	Poison Sanicle	Native	Annual	Apiaceae
<i>Silybum marianum</i>	<1	Milk Thistle	Introduced	Annual	Asteraceae
<i>Torilis arvensis</i>	<1	Hedge Parsley	Introduced	Annual	Apiaceae
<i>Triteleia laxa</i>	<1	Ithuriel's Spear	Native	Perennial	Liliaceae

Thirty-three species total. Sampling conducted April 2005 by point count in 17-m radius circular plots, 280 points/plot; rare species, present but not hit, are not included (Bartolome et al. unpublished data).

change over multiple years (Bartolome 1989a). Climate is the primary driver of change at the two smaller temporal scales (George et al. 2001; Jackson and Bartolome 2002), whereas other factors, often anthropogenically influenced, cause long-term changes.

INTRAANNUAL

Beginning with the first rainfall of 1.5 cm or more within a single week (usually between early September and late November), most of the annual grasses and forbs start germinating from seed, which has been dormant through the summer. Species composition is strongly affected by environmental conditions during fall germination and establishment (Bartolome 1976). Significant changes occur in numbers of plants and biomass per unit area as the growing season progresses.

Whereas rainfall patterns control the start and finish of the growing season, temperature determines the rate of biomass production (George et al. 2001). Following germination, established seedlings grow rapidly when temperatures are >15°C, more slowly if temperatures are cool (5°C to 10°C; George et al. 2001). Timing of germination and initial growth can dramatically affect biomass production because early rains generally coincide with warm fall temperatures, causing rapid growth over a longer fall growing period (George et al.). During the winter months, there is slow above-ground vegetative growth and root development. Warmer temperatures, longer days, and higher light levels in the spring (generally February 15–March 15 when average weekly temperatures are >7°C) stimulate rapid growth of above-ground vegetative and flowering parts (George et al.). Peak canopy biomass generally occurs during seed set in late spring, when most of the available soil moisture has been used (Duncan 1975). A 19-year study at Hopland REC by Heady (see Pitt 1975; Pitt and Heady 1978) showed that March 1 biomass averaged 900 kg ha⁻¹ and June 1 biomass, 3,090 kg ha⁻¹. Year-to-year variation exceeded 50% of both the March and the June means.

Biswell and Graham (1956) reported more than 20 seedlings per square centimeter after germination, but it is more likely that the long-term average is 3 to 5 per cm²

(Heady 1958). Both papers reported 10% to 90% mortality during the growing season, depending on species. Relative densities of *Bromus hordeaceus* and *B. diandrus* tended to increase during the growing season, whereas those of shorter plants decreased.

A 2-year study of seedling establishment and plant numbers at Hopland REC by Bartolome (1979) showed that near-maximum seedling densities for most species occurred by the second week of the growing season. However, seedlings of *Aira caryophylla*, *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 years, but biomass did not. Seed bank numbers far exceeded seedling numbers in most species, suggesting that environmental factors exert more influence on plant densities than does seed supply.

The period of rapid spring growth brings on a progression of different dominant species. Forbs such as *Agoseris heterophylla*, *Lasthenia californica*, *Hypochoeris glabra*, *Lotus*, *Orthocarpus*, and *Trifolium* flower and mature early, at about the same time. Among the grasses, *Aira caryophylla* and *Briza minor* set seed early, *Vulpia* later, and *Bromus hordeaceus* and *Bromus diandrus* later still. *Avena barbata* and *Erodium* flower and seed throughout the spring (Heady 1977). In summer, the dominant annuals succumb to desiccation, leaving only seeds to start the process over again when rains resume. Some summer-growing annuals are present, such as *Aristida oligantha*, *Gastridium ventricosum*, *Taeniatherum caput-medusae*, *Hemizonia*, *Madia*, *Lactuca*, *Eremocarpus setigerus*, and *Centaurea solstitialis* (Heady; Bartolome et al. 2002).

Savelle and Heady (1970) investigated the normal growth patterns of eight annual species in an outdoor pot study. The period of maximum growth rate varied from early March to early May. Under drying spring weather, rapid growth rates may end abruptly. Flower initiation began in early February in *Erodium botrys* but did not start until April for *Vulpia myuros* var. *hirsuta*. Flowering periods were as short as 1 month for *Aira caryophylla* and as long as 3 months for *Avena barbata* and *E. botrys* (Savelle 1977).

Individual species attain maximum biomass at different times from mid April to early June (Ratcliff and Heady 1962),

TABLE 14.4
 Combined Species Composition and Percentage Relative Cover for Five "Relictual Bunchgrass" Plots at Vasco Caves
 Regional Preserve, Eastern Contra Costa County

<i>Scientific Name</i>	<i>% Relative Cover</i>	<i>Common Name</i>	<i>Origin</i>	<i>Life Form</i>	<i>Family</i>
<i>Lolium multiflorum</i>	29	Italian Rye-grass	Introduced	Annual	Poaceae
<i>Bromus hordeaceus</i>	15	Soft Brome	Introduced	Annual	Poaceae
<i>Nassella pulchra</i>	7	Purple Needlegrass	Native	Perennial	Poaceae
<i>Erodium botrys</i>	7	Broad-leaf Filaree	Introduced	Annual	Geraniaceae
<i>Bromus diandrus</i>	7	Ripgut Brome	Introduced	Annual	Poaceae
<i>Bromus sterilis</i>	5	Sterile Brome	Introduced	Annual	Poaceae
<i>Avena fatua</i>	5	Common Wild Oats	Introduced	Annual	Poaceae
<i>Avena sp.</i>	5	Wild Oats	Introduced	Annual	Poaceae
<i>Geranium dissectum</i>	3	Cutleaf Geranium	Introduced	Annual	Geraniaceae
<i>Hypochaeris glabra</i>	2	Smooth Cat's Ear	Introduced	Annual	Asteraceae
<i>Avena barbata</i>	2	Slender Wild Oats	Introduced	Annual	Poaceae
<i>Carduus pycnocephalus</i>	2	Italian Thistle	Introduced	Annual	Asteraceae
<i>Erodium cicutarium</i>	2	Redstem Filaree	Introduced	Annual	Geraniaceae
<i>Bromus madritensis</i> <i>ssp. madritensis</i>	1	Foxtail Brome	Introduced	Annual	Poaceae
<i>Bromus madritensis</i>	1	Foxtail Brome	Introduced	Annual	Poaceae
<i>Erodium moschatum</i>	1	White-stemmed Filaree	Introduced	Annual	Geraniaceae
<i>Torilis nodosa</i>	<1	Hedge Parsley	Introduced	Annual	Apiaceae
<i>Vulpia bromoides</i>	<1	Brome Fescue	Introduced	Annual	Poaceae
<i>Bromus sp.</i>	<1	Brome	Introduced	Annual	Poaceae
<i>Leymus triticoides</i>	<1	Creeping Wildrye	Native	Perennial	Poaceae
<i>Achyrrachaena mollis</i>	<1	Blow Wives	Native	Annual	Asteraceae
<i>Trifolium oliganthum</i>	<1	Few-flowered Clover	Native	Annual	Fabaceae
<i>Achillea millefolium</i>	<1	Common Yarrow	Native	Perennial	Asteraceae
<i>Lotus wrangelianus</i>	<1	Chilean Trefoil	Native	Annual	Fabaceae
<i>Amsinckia menziesii</i> <i>var. intermedia</i>	<1	Orange-flowered Menzies' Fiddleneck	Native	Annual	Boraginaceae
<i>Bromus sterilis/madritensis</i>	<1		Introduced	Annual	Poaceae
<i>Hordeum murinum</i> <i>ssp. leporinum</i>	<1	Foxtail Barley	Introduced	Annual	Poaceae
<i>Marah fabaceus</i>	<1	Wild-cucumber	Native	Perennial	Cucurbitaceae
<i>Medicago polymorpha</i>	<1	Bur Clover	Introduced	Annual	Fabaceae
<i>Ranunculus californicus</i>	<1	California Buttercup	Native	Perennial	Ranunculaceae
<i>Castilleja exserta</i>	<1	Purple Owl's Clover	Native	Annual	Scrophulariaceae
<i>Chlorogalum pomeridianum</i>	<1	Soaproot	Native	Perennial	Liliaceae
<i>Dichelostemma capitatum</i>	<1	Bluedicks	Native	Perennial	Liliaceae

(continued)

TABLE 14.4 (continued)

Scientific Name	% Relative Cover	Common Name	Origin	Life Form	Family
<i>Eremocarpus setigerus</i>	<1	Turkey Mullein	Native	Annual	Euphorbiaceae
<i>Galium aparine</i>	<1	Common Bedstraw	Native	Annual	Rubiaceae
<i>Galium parisiense</i>	<1	Wall Bedstraw	Introduced	Annual	Rubiaceae
<i>Hirschfeldia incana</i>	<1	Shortpod Mustard	Introduced	Perennial	Brassicaceae
<i>Hordeum</i> sp.	<1	Barley	Introduced	Annual	Poaceae
<i>Lupinus bicolor</i>	<1	Bicolored Lupine	Native	Annual	Fabaceae
<i>Melica californica</i>	<1	California Melic	Native	Perennial	Poaceae
<i>Plagiobothrys nothofulvus</i>	<1	Rusty Popcorn Flower	Native	Annual	Boraginaceae
<i>Trifolium willdenovii</i>	<1	Tomcat Clover	Native	Annual	Fabaceae
<i>Vulpia myuros</i> var. <i>hirsuta</i>	<1	Foxtail Fescue	Introduced	Annual	Poaceae

NOTE: Forty-three species total. Sampling conducted April 2005 by point count in 17-m radius circular plots, 280 points/plot; rare species, present but not hit, are not included (Bartolome et al. unpublished data).

for example, in 1960 at a site near Berkeley: *Bromus hordeaceus* on April 24, *Erodium cicutarium* on April 30, *Medicago hispida* on May 8, *B. diandrus* on May 21, *Avena fatua* on 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 maturity: in 1 week, 79% of the *Erodium* biomass disappeared.

Maranon and Bartolome (1994) recorded seasonal changes in aboveground biomass at an ungrazed site in the San Francisco Bay Area that showed the normal pattern of rapid spring growth after the slower winter period. Vegetation dominated in January by *Bromus diandrus* gradually increased proportionally in *Avena* and *Lolium* and decreased in *B. hordeaceus*.

Estimates of seed bank populations in California annual grassland vary widely, ranging from 340 seeds m⁻² (Sumner and Love 1961) to 200,000 seeds m⁻² (Young and Evans 1989; Table 14.5). Buried seeds may live for several years. Major and Pyott (1966) found a poor correspondence between seed numbers below and the vegetation above. Obviously, not all species that can occur in the vegetation over a period of years will be evident at any one time. After extensive literature review 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. This conclusion differs from that of Peco et al. (1998), who found a high similarity between seed bank and plant composition in Spain.

Most viable seed produced by valley grassland annual species germinates the following fall, resulting in limited

seed reserves (Major and Pyott 1966; Bartolome 1979). Working at Hopland REC, Ewing and Menke (1983b) found that although simulated short drought periods and early onset of summer drought reduced seed production in *Bromus hordeaceus* and *Avena barbata*, seeds were produced even during severe drought conditions. Seed weights and germination rates in the two grasses declined only under extreme and prolonged drought conditions. Seabloom et al. (2003a) found that two native annual forbs were strongly seed-limited in serpentine grassland.

The characteristics of nutrient cycling are of particular interest in annual grassland because all minerals (except for those in the seed) are returned to the environment each year. Fertilization of annual grassland has been researched for over four decades, giving much fundamental knowledge of the cycling of the major minerals (Jones 1974). Few data are available for potassium, calcium, and the micronutrients, however.

Jones and Woodmansee (1979) reviewed the many interacting factors controlling cycling of nitrogen, phosphorus, and sulfur. Woodmansee and Duncan (1980) and others showed that nitrogen flows in an open system, in which much is lost and gained, whereas phosphorus flows in a closed system, with relatively little loss or gain. The cycling characteristics of sulfur are intermediate between those of nitrogen and phosphorus (Caldwell, Menke, and Duncan 1985).

Few studies have quantified nutrient content and productivity below ground. Jackson et al. (1988) followed the flow of nitrogen in plants and soil for a year at the Sierra Foothill Research and Extension Center (SFREC) on the eastern side of the Sacramento Valley. They found that plants accumulated nitrogen primarily in fall and early spring when the content of soil moisture was high, temperatures were moderate, and

TABLE 14.5
Estimates of Germinable Seed Found in Valley Grassland Soils

Location	Germinable Seeds/m ²	Reference
Hopland REC	32,000–160,000	Heady (1956a)
Hopland REC	29,760	Heady and Torell (1959)
Hopland REC	64,000	Bartolome (1979)
Winters, Yolo County	8,480–12,640	Major and Pyott (1966)
Sonoma County	15,680–20,800	Sumner and Love (1961)
Mariposa County	23,504	Sumner and Love (1961)
Kings County	340	Sumner and Love (1961)
Sierra Foothill REC	60,000–200,00	Young and Evans (1989)

NOTE: Adapted from Young and Evans (1989).

the plants were growing actively in the vegetative stage. Surprisingly, Jackson et al. found that significant amounts of nitrogen were mineralized from detritus during the dry season. With the first fall rains, significant amounts of nitrate were flushed out of the system, which helps explain the large nitrogen losses reported for annual grassland by Woodmansee and Duncan (1980).

Soil microbes play an important part in nutrient cycling and affect the availability of nutrients to plants. For example, the annual grassland ecosystem has 51% of its nonsoil organic matter tied up in microbial biomass, which may lead to significant competition for nitrogen among higher plants (Jackson et al. 1988). Steenwerth et al. (2003) found that soil microbial communities under relict and restored perennial bunchgrass stands were different from those under formerly cultivated annual grasslands in Monterey County. Although microbial biomass varied widely in their 10 perennial grassland sites with distinct differences between relict and previously cultivated sites, all 16 annual grassland sites showed a very similar microbial profile regardless of time since last tilling (8 to 50 years), suggesting that some characteristic of annual grassland (e.g., composition and/or productivity) influences the microbial community. Subsurface soil bacterial communities (1–4 m) differed significantly from and were less diverse than bacterial communities at the soil surface in 2 Santa Ynez perennial grassland sites (Lamontagne et al. 2003). These subsurface bacterial communities may play an important role in nutrient and carbon cycling.

Fossorial mammals also affect nutrient dynamics in grasslands. At Hopland REC, gopher-disturbed soil exhibited larger pools of NH₄ and NO₃ and higher nitrification potential (Canals, Herman, and Firestone 2003). These higher levels of plant-available N were probably transient, however. Gophers affected nitrogen cycling primarily by removing plants, thereby reducing plant uptake of inorganic N and root-enhanced microbial immobilization of NO₃-N.

INTERANNUAL

The interannual 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. If a germinating rain falls during summer or early fall, plants that emerge may not survive the drought period that is likely to follow. *Erodium* is an exception, often surviving such a “false break of season” (George et al. 2001) and subsequently dominating that year. To dominate, grasses require continuous rainfall or at least dry periods <2 to 3 weeks long (Heady 1977). Surprisingly, Jackson and Bartolome (2002) found no evidence in their 6-year dataset for the widely held belief that weather can reliably predict dominance by grasses, *Erodium*, or legumes.

At any given site, the date of peak standing crop and the pattern of biomass increase can vary widely from year to year (Fig. 14.4). During the winter until about the first of March, green herbage might be scarce in some years and abundant in others. In years when *Erodium* dominates, peak standing crop comes earlier than in years when grass species dominate. Summer-growing annuals may add significant biomass in some years and on some sites (George et al. 2001). Biomass at the end of the growing season can differ several-fold among years. Duncan and Reppert (1960) reported a production range of 775 to 2,900 kg ha⁻¹ over a 25-year period on the San Joaquin Experimental Range. At Hopland REC, above-ground standing crop on March 1 varied between 240 and 2,180 kg ha⁻¹, but high March weights were not always followed by high June weights (Pitt 1975; Pitt and Heady 1978).

Three sets of data on biomass, productivity, botanical composition, and weather were analyzed by Murphy (1970) for the purposes of developing predictive relationships at Hopland REC. He found that precipitation in November correlated ($r^2 = 0.7$) with forage yield several months later.

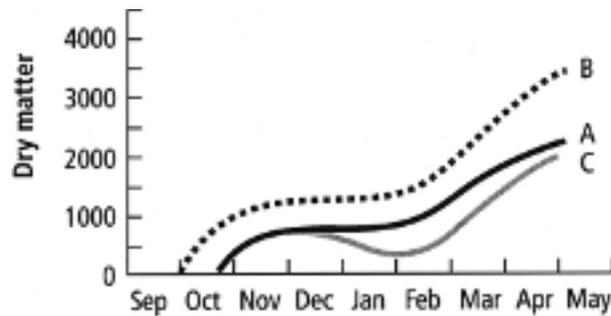


FIGURE 14.4 Valley grassland biomass production curves (kg ha^{-1}) for three different weather patterns, using data from the San Joaquin Experimental Range. Curve A represents an average fall, winter, and spring; curve B, a warm, wet fall followed by an average winter and spring; curve C, an average fall, cold winter, and average spring. Adapted from George et al. (2001).

In contrast, Duncan and Woodmansee (1975), using 24 years of data on the San Joaquin Experimental Range, found 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 REC, also obtained poor relationships between yield and precipitation alone. Inclusion of temperatures and periods without precipitation improved the regressions and explained more of the variation. For example, 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). In the San Francisco Bay Area, Ewing and Menke (1983a) studied drought effects on production of *Bromus hordeaceus* and *Avena barbata*, finding that biomass at the end of the growing season was not significantly affected by three experimental drought regimes.

Long-Term Directional Change

SUCCESSION AND INVASIONS

Generalizations about succession are difficult due to the high degree of temporal variation in the grassland that tends to override predictable longer term patterns of change. Additionally, the site dependency and time dependency of those changes means that considerably more empirical information is needed to make generalizations.

Grassland ecologists have recently developed several models that better describe succession than did the older, equilibrium-type models. The state-and-transition model (Westoby, Walker, and Noy-Meir 1989) provides a powerful general approach that currently is being adapted to accommodate the frequently observed discontinuous and nonreversible vegetation changes characteristic of arid rangelands. Many of the supposed differences between equilibrium and nonequilibrium approaches are dependent on spatial and temporal scales (Briskie, Fuhlendorf, and Smeins 2003).

Jackson and Bartolome (2002) subjected the same spatially and temporally replicated data set used by Bartolome, Stroud, and Heady (1980) to develop a state-and-transition model for the grassland. They found that an appropriate model was highly complex but that several environmental variables explained the details of vegetation change. Interactions among site and weather were the most important variables driving vegetation change. Only a few sites responded to residual dry matter (RDM). They suggest that nonequilibrium models are best for this vegetation type.

Over the last 3 centuries, California's grasslands have experienced multiple waves of plant invasions (Heady et al. 1991). Despite the profound and usually unwanted impacts of these invasions, accidental introductions of nonnative species into the annual grassland continue to occur, with some species having the potential to become pernicious weeds (Randall et al. 1998; Hrusa et al. 2002). Recent successful invasive grass species include *Taeniatherum caput-medusae*, *Aegilops triuncialis*, and *Brachypodium distachyon* (Heady et al.; Peters, Johnson, and George 1996).

Allen-Diaz (2000) reported that 1,023 nonnative, naturalized species are known to occur in California, 17.4% of the state's plant species. Sixty-five percent of these nonnatives come from Eurasia and North Africa. The plant families with the largest number of nonnative species are the Poaceae (181 species, 40% of the grass species found in California), the Asteraceae (151 species), the Fabaceae (90 species), and the Brassicaceae (63 species; Randall, Rejmánek, and Hunter 1998). The majority of nonnative species occupy low-elevation habitats, and approximately 400 of these nonnative taxa are part of the California grasslands.

The invasion of California's grasslands does not affect the flora alone; ecosystem processes and services have likely been altered as well. Native perennial bunchgrasses produce deep root systems (≥ 60 cm) and use soil moisture throughout the summer dry season. In contrast, nonnative annual grasses and forbs concentrate root growth in the upper 30 cm of the soil profile and senesce early in the dry season (Hull and Muller 1977; Holmes and Rice 1996). Because of these life-history differences, the putative conversion of California's grasslands from perennial bunchgrasses to annuals may have produced an increase in moisture remaining in the soil during the dry season (Holmes and Rice; Dyer and Rice 1999). The more recent invasion of Central Valley and foothill grasslands by the deep-rooted, summer annual star-thistle, *Centaurea solstitialis*, may be reversing this increase in soil moisture. Gerlach (2004) estimated that *C. solstitialis*' summer use of moisture throughout the soil profile causes depletion of 15% to 25% of the mean annual precipitation on invaded sites.

PATHOGENS AND ENVIRONMENTAL CHANGES

The role of plant pathogens in the California annual grassland has not been well studied, despite the fact that

pathogens can change, inter alia, community structure and competitive interactions. The aphid-dispersed barley yellow dwarf virus (BYDV) infects many introduced and native grasses in California (Griesbach et al. 1990; Malmstrom 1998) and reduces survivorship and seed yield in some species. Malmstrom (1998) hypothesizes that BYDV may affect competition between nonnative annual grasses and some perennial bunchgrasses in favor of the annuals. Carsten et al. (2001) found that crown rust greatly reduced the biomass and reproductive output of *Avena fatua*, shifting competitive outcome in favor of *Nassella pulchra* when the two species were grown together.

Environmental changes, such as climate change and pollution, are likely to have significant impacts on the Valley Grassland. Zavaleta et al. (2003a, b) investigated the responses of annual grassland species to 3 years of increased CO₂, warming, nitrogen deposition, and rainfall. The two dominant functional groups, annual grasses and forbs, responded differentially in production and abundance to various combinations of these experimental factors. Whereas realistic combinations of climate change factors had little effect on species diversity, significant changes in functional group relative abundance occurred under elevated CO₂, warming, and precipitation, the largest being a 50% increase in forbs. Nitrogen deposition from air pollution appears to have enabled nonnative annual grasses to invade serpentine grasslands in the San Francisco Bay Area. In the absence of grazing, *Lolium multiflorum* in particular crowded out small native annual forbs, host plants for the threatened Bay checkerspot butterfly (*Euphydryas editha bayensis*; Weiss 1999). Ozone pollution differentially affects growth patterns and mycorrhizal colonization in populations of *Elymus glaucus* from high- and low-ozone environments (Yoshida, Gamon, and Andersen 2001).

Spatial Scales

The Valley Grassland also exhibits huge spatial variability. Conventional spatial scales include microsite (~1 cm²), the scale of seed germination and seedling establishment; patch (~1 m²), the scale of competitive interaction, animal effects, and influences of woody overstory; and site (~1 ha), the scale of topographic, climatic, and edaphic variation, and of effects of land-use history, grazing, and fire (Bartolome 1989a).

An emerging area of research is spatial patterning and its effects on species numbers and distribution. Plants being sessile organisms, interactions are typically most intense between neighboring individuals (Fehmi 1998). As a result, local spatial patterns may prove useful in understanding plant community mechanisms and processes. Specific species distribution patterns may reflect competitive or facilitative interactions, allelopathy, seed dispersal, predation, and grazing. Using the dominant grasses *Lolium multiflorum* and *Bromus hordeaceus* in a spatial aggregation experiment, Fehmi et al. (2001) demonstrated that, at small

scales, species composition was more important than spatial distribution in determining productivity.

Some native species are restricted to hummocks (shallower soils, lower cation-exchange capacity, and greater percentage of sand) in serpentine grassland; other native species are restricted to the exotic-dominated serpentine grassland matrix (Gram et al. 2004). Small-scale variations in soil-surface characteristics have been shown to be very important for maintaining diversity in the Mediterranean (Naveh and Whittaker 1979), with only a small comparable research base, primarily on serpentine, for California.

MICROSITE

In two Sierran foothill sites, Young et al. (1981) exhaustively investigated quantitative aspects of seed availability for germination in relation to microtopography. At Hopland REC, [MB2] Bartolome (1979) examined the effects of small-scale differences in mulch amounts on germination and seedling establishment. Germinable seed density in 2 sequential years was 6.7 and 6.1/cm⁻².

Mulch influences germination and seedling establishment through modification of several microenvironmental factors. Most seeds germinate on the soil surface or at depths to 1 cm. Mulch favors microorganisms, seedlings, water infiltration, rapid decomposition, and other factors, but a 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.

PATCH

Competition and the Influence of a Woody Overstory

In a community as diverse as the Valley Grassland, it is not surprising that many mechanisms mediate competitive relationships, thereby maintaining species coexistence. Disturbance, such as herbivory and fire, spatial and temporal variation of limiting resources, and dispersal dynamics all help maintain the diversity of California's grasslands (Rice 1989).

Much experimental effort has been expended on evaluating the effects of nonnative annual species on the native perennial bunchgrass *Nassella pulchra* (Bartolome and Gemmill 1981; Nelson and Allen 1993; Dyer and Rice 1997a, 1999; Hamilton Holzapfel, and Marshall 1999; Fehmi, Rice, and Laca 2004). The general conclusion is that in most circumstances, nonnative annuals reduce seedling establishment, survival, and reproduction of *N. pulchra*, either due to competition for water (Hamilton, Holzapfel, and Marshall 1999) or light and water (Dyer and Rice 1999). Exceptions may occur during years of heavy rainfall when soil moisture is not limiting and in years of drought

early in the growing season when nonnative annual seedlings are reduced to a greater extent than *N. pulchra* seedlings (Hamilton Holzapel, and Marshall).

Recent work by Seabloom et al. (2003b) suggests that native perennial grasses other than *Nassella pulchra* may generally outcompete exotic annuals, although Brown and Rice (2000) reported that *Vulpia myuros* reduced seedling survival and biomass of a similar suite of native perennial grasses. Dennis (1989) found that *Poa secunda* spp. *secunda*, *Melica californica*, and *Koeleria macrantha* responded adversely to competition with annuals but that light and water did not appear to be the limiting factors.

Other work addresses competition between annual species, both native and introduced. 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). Bell and Muller (1973) convincingly demonstrated the dominance of *Brassica nigra* over annual grasses through allelopathic toxins. Seasonality mediated competition between two species of *Erodium*: *E. botrys* dominated following fall drought, whereas *E. brachycarpum* dominated following spring drought (Rice and Menke 1985). A study of coexistence between *Bromus hordeaceus*, *Lolium multiflorum*, and *A. fatua* at Jasper Ridge concluded that although *A. fatua* remains dominant due to its large seeds and seedlings, it could not reach sufficient density to exclude the two smaller species under normal soil nitrogen levels (Gulmon 1979). The invasive success of *C. solstitialis* in Californian annual grasslands, as compared to less successful congeners, is based in part on its ability to maintain some minimum level of reproduction under intense competition from annual grasses and to reproduce at maximum fecundity when competition is limited by soil disturbance, grazing, and summer senescence of annual grasses (Gerlach and Rice 2003). In the Jasper Ridge serpentine grassland, three annual forbs—*Plantago erecta*, *Lasthenia californica*, and *Calycadenia multiglandulosum*—each performed significantly better against one of the other study species when grown in soil from patches where the better competitor occurred most abundantly (Reynolds et al. 1997). Competitive outcomes correlated with heterogeneity in soil moisture and depth inherent to the patches and with differences in soil nitrate availability, which was strongly affected by which species grew in a patch. Temporal habitat partitioning may also play an important role in coexistence: *P. erecta* and *L. californica* mature by May, whereas *C. multiglandulosum* flowers in July–August.

[MB2]

Parker and Muller (1982) studied vegetation differences under and adjacent to *Quercus agrifolia* in southern California grasslands. Whereas *Avena fatua* was prominent in the grassland, *Bromus diandrus* was prominent under the tree canopies along with the evidently allelopathic *Pholisoma auritum*. McClaran and Bartolome (1989) described variations in herbs along a rainfall gradient between 40 and 90 cm yr⁻¹ as part of study examining oak canopy effects. They

found that annual herb composition varied considerably among grassland sites and that the oak canopy contributed significantly to overall site diversity.

Effects of Animals

Nondomesticated animals dramatically influence grassland structure and processes, primarily through herbivory and soil disturbance. The grazing and burrowing of three common small mammals, *Thomomys bottae* (Botta's pocket gopher), *Microtus californicus* (California vole), and *Spermophilus beecheyi* (Beechey ground squirrel), change biomass production, species composition, and invasion dynamics in the California annual grassland (Lidicker 1989). A fourth rodent, the little-studied granivore, *Reithrodontomys megalotis* (western harvest mouse), may also play an important role (Lidicker 1989), as may the cumulative effects of many other species (Schiffman 2000).

Burrowing by Botta's pocket gophers disturbs huge quantities of soil in California's grasslands. Cox, Contreras, and Milewski (1995) estimated that gopher mining on the San Diego coastal terraces results in turnover of >1% of the upper 20 cm of soil per year, whereas at Jasper Ridge as much as 30% of the total serpentine grassland area may be disturbed by gophers in a single year (Hobbs and Mooney 1985). In a summary of their long-term study of serpentine grassland at Jasper Ridge, Hobbs and Mooney (1995) concluded that gopher disturbance was a major, albeit complex, factor in plant community variation. At Hastings Reservation, where gopher densities are among the highest in the state, Stromberg and Griffin (1996) found that mean number of nonnative annual seedlings was higher and survivorship and growth of perennial grass seedlings lower on gopher tailings than on undisturbed soil. Dyer and Rice (1997a) also found that gopher activity significantly reduced *Nassella pulchra* survival at Jepson Prairie Reserve. Seabloom and Richards (2003) demonstrated a positive feedback loop between pocket gophers and annual plants in restored grassland; the gophers create persistent and distinct plant communities over large areas. In contrast, gophers inhibit the establishment of the invasive annual grass, *Aegilops triuncialis*, by burying patches of *A. triuncialis* seedlings, killing some and simultaneously interfering in a fungal-plant interaction. A fungus accelerates the germination and establishment of *A. triuncialis* by softening its seed head, but *A. triuncialis* seedlings that survive burial under gopher tailings produce uninfected seeds, which may decrease subsequent seedling establishment (Eviner and Chapin 2003).

Borchert and Jain (1978) documented the considerable effects that seed predation by the California vole and the house mouse (*Mus musculus*) had on plant numbers and competitive outcomes in annual grassland near Davis. Competitively superior but preferred *Avena fatua* numbers declined, while *Lolium multiflorum*, *Hordeum murinum* ssp. *leporinum*, and *Bromus diandrus* increased in size and reproductive output. In a *Microtus californicus* enclosure

experiment, Cockburn and Lidicker (1983) found that 7 of 43 plant species were present only in exclosures, 10 species were more abundant in exclosures, and 4 of those 10 flowered exclusively in exclosures. Another study found that at peak population densities, *M. californicus* destroyed 20% of the grassland vegetation through runway construction during the dry season (Ford and Pitelka 1984). Herbivory by *M. californicus* reduced *Erodium* seedling survival to about 20%, compared with almost 100% survival in *Erodium* seedlings protected from voles, and *Erodium* effective reproductive rates fell by a factor of 10 (Rice 1987). In Coast Range grassland, Fehmi and Bartolome (2002) found that areas surrounding *M. californicus* burrows exhibited greater species richness than areas without burrows. They also suggested that reduced livestock grazing pressure could increase *M. californicus* populations, which in turn increases vole predation on annual grass seeds.

The Beechey ground squirrel digs extensive burrow systems and may consume 3% to 7% of primary productivity (Lidicker 1989). Giant kangaroo rat (*Dipodomys ingens*) burrows at Carrizo Plain occupy as much as 32% of the grassland. In addition, cover of nonnative annuals was significantly greater, and cover of natives significantly less, around their burrows than in intermediate areas (Schiffman 1994). Hobbs (1985) found that harvester ants (*Veromessor andrei*) are the major seed predators in the Jasper Ridge serpentine grassland and concluded that ant foraging significantly reduced the abundance of preferred plant species.

SITE

Topographic and Climatic Gradients

The annual grassland responds to site variation in soil nutrients (McCown and Williams 1968) and temperature and moisture. McNaughton (1968) showed that the structure of the annual grassland was also correlated with slope, aspect, and soil even over small distances. Detailed analyses substantiating these results exist for only a few locations and are very scarce for slope and aspect.

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 baseline information by the State Cooperative Soil-Vegetation Survey (U.S. Forest Service 1954; University of California 1959). As a general rule, perennial species and higher biomass production are characteristic near the coast and in areas of higher precipitation than in the drier inner valleys. Janes (1969) studied species composition and production of 20 grassland sites at approximately 80-km intervals along a precipitation gradient (12.5–200 cm annually), from the southeastern end of the San Joaquin Valley (Kern County) to the north Pacific coast (Humboldt County). Sites were selected for uniform slope (<35%), southerly aspect, no evidence of fire or grazing within 3 years, and with A and B soil horizons >50 cm deep. Janes encountered 124 species, but only seven occurred in four or more of his sites. Species diversity was higher between

50 and 100 cm of annual precipitation than at greater or lesser amounts of rainfall. The seven dominant annual species were distributed, on the basis of rainfall, as follows:

- <20 cm: *Bromus madritensis* ssp. *rubens*; *Erodium cicutarium*
- 20–80 cm: *Avena fatua*; *B. diandrus*; *B. hordeaceus*; *E. botrys*
- >80 cm: *A. barbata*; *B. hordeaceus* (equal abundance in 20–80 cm); *E. botrys* (equal abundance in 20–80 cm).

Burcham (1975) compared the vegetation among 38 sites located in the foothills of the Sierra Nevada mountains, from Sacramento to Fresno and in the Coast Ranges from Santa Clara to Monterey counties. Like Janes (1969), he found *Bromus hordeaceus* to be the most typically dominant species, forming a significant portion of the cover in 30 of the 38 locations. *Erodium* occurred in 31 sites. *B. diandrus* and annual *Vulpia* species were in 21 and 19 sites, respectively, though neither with high cover.

Bartolome et al. (1980) described the composition of nine sites scattered throughout the annual grassland, along a rainfall gradient of 16–160 cm annual precipitation. They concluded that the grassland could be treated as three units for management purposes. Areas with >100 cm annual precipitation usually were characterized by perennial grasses with annual species between bunches even under heavy grazing. The most common perennial grass of these sites is *Danthonia californica*. The annuals *Bromus hordeaceus* and *Erodium botrys* characterized sites with 65–100 cm annual precipitation, and *B. madritensis* ssp. *rubens* and *E. cicutarium* occupied sites receiving <25 cm annual precipitation.

Proportional representation of perennials and annuals, and of introduced versus native species, varies drastically with location. The nine sites studied by Bartolome et al. (1980) showed a general decrease in species richness with decrease in rainfall (Heady et al. 1991). Perennial species were more common with higher rainfall. Relict stands of perennial grasses are rare away from the coast, and all contain substantial numbers of introduced annuals (Heady 1977).

Edaphic Factors

California annual grassland is found on a wide variety of soils (Evans and Young 1989), sometimes closely situated in a complex mosaic. Barry (1972) lists 195 soil series on which grassland occurs. Most California grassland soils are noncalcareous Mollisols, medium to heavy in texture, granular in structure, moderate in organic matter content, and ~0.5 m deep (Heady 1977).

Serpentine-derived soil supports a distinctive flora and so far has resisted invasion by most Mediterranean annuals. As a result, serpentine sites have attracted much research attention. Although chemical and physical characteristics of ser-

serpentine soils can vary widely from site to site (Koenigs et al. 1982), typically they are magnesium-rich, low in calcium (creating an unfavorable Ca:P ratio) and other elements important to plant growth, and have high concentrations of heavy metals such as nickel that are toxic to most plants (Kruckeberg 1984). Hobbs and Mooney (1995) summarized an 11-year study of the Jasper Ridge serpentine annual grassland, finding that plant species abundances exhibited a variety of responses to rainfall variability and gopher disturbance. Harrison (1999) compared native versus introduced species diversity on serpentine and nonserpentine grasslands, reporting that native diversity was much higher on serpentine and tended to be related to the severity of the site. She encountered 69 native and 20 nonnative taxa on serpentine, compared to 57 natives and 34 exotics on non-serpentine. In addition, fall fire and year-round grazing increased native species richness on serpentine grasslands but total and nonnative species richness on non-serpentine grassland (Harrison, Inouye, and Safford 2003).

LAND-USE HISTORY, LIVESTOCK GRAZING, AND MANAGEMENT OF RDM

Bartolome (1989b) suggested that cultivation had an impact on the original California grassland second only to the introduction of the nonnative flora. In their long-term study of Hastings Reservation grassland, Stromberg and Griffin (1996) found that cultivation history had a strong impact on current species composition. Stands dominated by perennial bunchgrasses were restricted to uncultivated sites, whereas former agricultural fields were dominated by nonnative grasses and forbs. Robertson (2004) concurred, determining that for eastern Alameda and Contra Costa counties, a history of dry-land farming was negatively associated with presence of native perennial grasses and native annual forbs. Stromberg and Griffin and Hamilton, Griffin, and Stromberg (2002) observed that *Nassella pulchra* appears to have difficulty recolonizing former agricultural fields.

Other land uses also affect species composition and invasive success. Roads can serve as conduits for the spread of non-native species. Invasion of nonserpentine foothill grassland by non-native species is correlated with proximity to roads (Gelbard and Harrison 2003). Percentage native cover and percent native species were greatest in plots >1,000 m from a road and least in plots 10 m from a road.

The first concerted ecological research studies in the annual grassland were directed toward understanding the forage base for livestock grazing (Bentley and Talbot 1951). Much of this work also established the primacy of site and weather as factors controlling production and composition. Numerous later studies and management practice have shown that the effects of grazing and its management are largely explained by the role of litter or residual dry matter (RDM; Bartolome et al. 2002).

Unlike many other grazed ecosystems, the annual grassland exhibits very little response to seasonality of grazing use. Grass species dominate the California annual grassland

in large part by reducing light availability for shorter stature forbs (George et al. 2001). Livestock grazing theoretically lessens this competitive advantage by removing grass biomass and thatch, and is often observed to increase the cover of broad-leaved species. However, this same response occurs with the removal of excess litter or RDM (Heady 1956a). More recently Jackson and Bartolome (2002) showed that the links of RDM levels to species composition were highly site dependent and year dependent. Under light grazing, taller species, such as *Avena fatua* and *Bromus hordeaceus*, dominate; with heavy grazing, shorter species prevail. Intensive grazing delays fall growth and reduces winter growth (Talbot and Biswell 1942; Bentley and Talbot 1951).

In the 1950s, Harold Heady conducted a series of experiments showing that fall RDM dramatically influenced biomass productivity and species composition in a high-rainfall (89 cm yr⁻¹) Mendocino County annual grassland site (Bartolome et al. 2002). With no RDM at the time of germination, *Aira carophyllea*, *Lasthenia californica*, *Hypochoeris glabra*, and *Triphysaria eriantha* dominated the vegetation on the site (Heady 1956a). When plant residue was left on the ground, the relative cover of *Bromus hordeaceus* increased from 1% to 37% in 3 years; when all the mulch was removed each year, the cover of *B. hordeaceus* remained at <2% (Heady 1965).

Subsequent research by Heady and others demonstrated a strong effect of RDM on biomass productivity in areas with an average annual rainfall >38 cm (Bartolome et al. 2002). Effects on species composition were mixed (Jackson and Bartolome 2002). There is little evidence about grazing effects on soil or on the efficacy of rotational systems.

With recommended intensities of livestock grazing, measured as the amount of RDM remaining, no soil erodes, productivity of biomass remains high, and floristic composition of the vegetation shows little change (Table 14.6). In fact, annual grassland withstands remarkably heavy short-term livestock use (Bentley and Talbot 1951; Heady 1961). Stocking rates two to three times 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 (Bartolome et al. 2002).

FIRE

Occasional fires in the grassland have little permanent effect. Burning apparently does not alter moisture content, temperature, and organic matter in soil where grazing has already removed most of the above-ground biomass. Few seeds are destroyed by grassland fires (Bentley and Fenner 1958). Many fire effects duplicate those of mulch removal by hand (Talbot, Biswell, and Hormay 1939; Heady 1956a), and none of the changes has been detected beyond the third year after burning. Parsons and Stohlgren (1989) found that burning a Tulare County grassland significantly decreased biomass of *Avena fatua* and *Bromus diandrus* one-

TABLE 14.6
Recommended Minimum Residual Dry Matter Levels for Dry Annual Grassland and Annual Grassland

Grassland Type	Percentage Slope			
	0–10	10–20	20–40	>40
Dry annual grassland	340	450	560	670
Annual grassland	560	670	790	900

NOTE: Dry matter levels in kg ha⁻¹ for dry annual grassland (average annual rainfall <30 cm) and annual grassland (average annual rainfall from 30 to 102 cm). Adapted from Bartolome et al. (2002).

to twofold. Once burning ceased, however, these nonnative grasses rapidly reestablished dominance. Similarly, species richness increased on serpentine and nonserpentine soils in the year following a fire but returned to prefire levels within 2 years (Harrison, Inouye, and Safford 2003).

Following fire, species composition sometimes shifts toward broad-leaved plants and away from annual grasses (Hervey 1949; Stromberg and Kephart 1996). Parsons and Stohlgren (1989) reported that fall and spring burns in an ungrazed, *Avena fatua*-dominated grassland in the foothills of Tulare County decreased the biomass of nonnative grasses but increased richness and biomass of alien and native forb species. Fire frequency may be an important factor though: Eller (1994) found that *Erodium* species increased in cover after a single burn but then decreased in cover after subsequent burns. Fire did not have consistent effects on seed banks of grassland species in coastal Marin grasslands (Alexander and D'Antonio 2003). One site exhibited a trend toward increased numbers of exotic grass and forb seeds after two burns, but after three burns, exotic grass seeds declined and native forb seeds increased. At a second site, in contrast, after four burns, annual grass seed numbers were significantly higher, and exotic forb seeds similarly showed an increasing trend.

Grazing is often justified by land managers as a fuel reduction tool but with little supporting evidence. On annual rangelands, recommended RDM levels (Table 14.6) are near the threshold for effective fire protection. On perennial-dominated grasslands with higher RDM standards, it may prove difficult to achieve both fire protection and protection of natives.

Conservation and Restoration Issues

Beginning in the late 1970s (with the Endangered Species Act of 1973), conservation of certain rare or endangered species became a priority for both nongovernmental organizations (NGOs) and state and federal land-management agencies. Many of the grasslands in the Central Valley are a mosaic of grasslands and seasonal wetlands that include vernal pools. These vernal pools support many of the most rare plants in California. As a consequence, many thousands of acres of

grassland came into conservation ownership or management as vernal pool species were protected by NGOs and government agencies (e.g., Jepson Prairie, Vina Plains, Beale Air Force Base, Carrizo Plain). Rare or endangered waterfowl (e.g., Aleutian Canada Goose) caused the U.S. Fish and Wildlife Service to acquire or protect many thousands of acres of grassland in the center of the Valley as winter foraging habitat for these geese and other waterfowl. Today, the San Luis Refuge Complex in the San Joaquin Valley and the Sacramento Refuge Complex in the Sacramento Valley protect diverse examples of grasslands that grow on a wide range of salt-affected soils.

The vast majority of the remaining acreage of grasslands in the Central Valley is under private ownership. Recent use of conservation easements (a legal restriction attached to the property's deed) that preclude development has been effective in protecting some privately owned grasslands.

In the California State Park System, current re-vegetation efforts concentrate on reestablishing native plant communities as the first step in restoring natural, native ecosystems. The California Public Resources Code requires restoration or maintenance of "native environmental complexes" in State Parks and "native ecological associations" in State Reserves. Department policy has further defined this as the condition prior to European influence, taking into account what would have evolved with climatic changes since that time. With current global warming trends, the best baseline time period is considered to be around 1300 AD, during the late Medieval Warming Period. Restoration of native grassland ecosystems includes re-establishing natural ecological cycles, such as fire and flooding, and planting of native taxa where seed sources are not present. Grassland restoration is summarized by Barry (2003).

Conservation Management

Without management, nonnative annual grasses will tend to become dominant to the near-exclusion of most native plants (Brown and Rice 2000). Intensive mowing and herbicide trials (Bugg, Brown, and Anderson 1997) showed that native perennials exhibit a range of responses and that weed management was possible within a stand of native grasses. In Santa Barbara County, experiments suggested that sowing



FIGURE 14.5 Early summer burning to control barbed goatgrass (*Aegilops triuncialis*) control and native perennial enhancement at Nunes Ranch, Contra Costa County.

native grass seed directly into annual-dominated grassland might create a native, perennial-dominated grassland (Seabloom et al. 2003b). However, over the large acreage of most grassland preserves, the only feasible management tools are livestock grazing, prescribed fire, and perhaps biological control (Carsten et al. 2001).

Historically, the primary goal of management for Central Valley grasslands has been the production of livestock. The goals of conservation management, in contrast, focus on high levels of biological diversity of native species and the habitat needs of target animal species. The current site-specific method of increasing native plant diversity is to reduce nonnative plant abundance through management actions (DiTomaso, Kyser, and Hastings 1999), for example, the timing of treatments that damage a target's invasive ability to form seed (Fig. 14.5). The abundance of *Centaurea solstitialis* and *Taeniatherum caput-medusae* has been significantly reduced at Vina Plains by timed grazing followed by prescribed burning in May or June when *T. caput-medusae* is completing seed production and *C. solstitialis* is beginning to flower. In Sugar Loaf Ridge State Park, after three prescribed burns, the cover of native perennial grasses increased from 6% to 21%, native forbs increased from 5% to 26%, and *C. solstitialis* decreased by 99% on burn plots (Hastings and Barry 1997). Similar increases were noted on a 600-acre burn plot at Folsom Lake State Recreation Area following three prescribed fires between 1998 and 2000. *Muhlenbergia rigens* stands increased in size where cool intensity burns occurred, and *C. solstitialis*, which dominated some transects, was absent in all transects by 2001 (Barry 2003).

Livestock grazing can be an effective tool for managing vegetation and some individual species. The timing (season and duration) and stocking rate, or density of animals in a pasture, will impact different species of plants differently (Dennis 1989). Bartolome et al. (2004) found that *Nassella pulchra* increased most with spring grazing, whereas *N. lepida* and *Danthonia californica* increased most when grazing was removed. In a 3-year study at Carrizo Plain, Kimball and

Schiffman (2003) found that clipping significantly reduced cover and richness of native annual forbs and *Vulpia microstachys*, whereas nonnative grass and forb species richness and cover remained largely unaffected. They posited that Mediterranean grassland species, long exposed to livestock grazing, have adaptations such as compensatory growth that enable them to recover from grazing, whereas native species generally lack these mechanisms.

One common objective of livestock grazing on preserves is to reduce the amount of RDM. This allows sunlight to reach the soil surface and stimulate germination of the seeds of native species. A more refined objective might be to target a particular invasive species such that its seeds are consumed by livestock, or it is trampled at a sensitive time in its life cycle. Timing is everything.

Real-world experience has shown that the best way to achieve conservation goals is for the grassland manager to clearly describe conditions on a pasture that are the desired goals, then allow the cattle operator to develop the details of the grazing prescription (stocking rate, duration, season, frequency). For example, the manager describes to the operator that he wants no less than 560 kg ha⁻¹ of RDM at the end of the grazing period and that the native grasses produce seed, or that certain wildflower species are abundant. Careful monitoring of relative abundances of plant species can result (over several seasons) in management prescriptions that can be tailored to site-specific goals.

Prescribed fire can also be used to remove RDM and promote native species (DiTomaso, Kyser, and Hastings 1999; Pollak and Kan 1998; Dyer 2002, 2003). By contrast with grazing, fire typically will completely remove all RDM. Many native wildflower species respond positively to a burn by increasing in abundance the season following the fire. However, many invasive weeds, such as *Centaurea solstitialis* and *Erodium*, increase dramatically following a fire. The timing of burns can have significant impacts on most plant species. Burning in the late summer or fall will remove RDM, but will have a lesser effect on reducing nonnative invasives compared to a late-spring burn that consumes much of the seed of invasives.

D'Antonio et al. (2002) reviewed the effects of fire and grazing on native grassland species in California by examining the results of 45 (19 fire, 17 grazing, 9 fire and grazing) mostly published studies. They concluded that the relationship between grazing and native grassland plants had not been clearly established, primarily because of the complex responses that varied among sites and years. They found that grazing benefited native populations in some studies but that a positive response was not universal among species or even within species across different locations. Although it is widely accepted that fire benefits native species, the review found that fire did not result in a straightforward increase of natives and decrease in exotics. Benefits from fire depended on frequency of burning and the presence of livestock. Native forbs benefited most from annual burning but not when grazing was included. Climate was more important

than type of burning in determining response of native perennial grasses (generally *Nassella pulchra*; see also Marty et al. 2003).

Genetics

Recent work on the genetics of grassland species has been driven largely by restoration concerns and consequently focuses on that favorite son, *Nassella pulchra*. Conservation geneticists are concerned about maintaining genetic variation within species and about preventing contamination of local ecotypes with material from nonlocal populations. Knapp and Rice (1994) laid out important genetics-based rules to follow when collecting and agronomically increasing native seed for restoration. They emphasized the need for collecting locally adapted seed and avoiding genetic contamination of local populations, for sampling as much of the genetic variation in a population as possible, and for avoiding genetic shifts in agronomically grown seed.

Population genetic studies examine quantitative traits (in common garden experiments) or genetic material (e.g., DNA or allozymes) to evaluate how populations from varied geographical, edaphic, or climatic areas differ. In common garden experiments, *Nassella pulchra* populations from Mendocino, Marin, and San Joaquin counties exhibited considerable variation in germination rates when subjected to mulch and moisture stress treatments (Bartolome and Gemmill 1981), and serpentine and non-serpentine *N. pulchra* populations differed in morphology, growth, and response to clipping (Huntsinger et al. 1996). In dry and wet common gardens, Adams et al. (1999) evaluated quantitative traits in three to six populations of four California native perennial grasses, finding differences in phenology and growth among the populations.

Using a DNA fingerprinting technique to examine 14 populations of *Nassella pulchra*, Larson et al. (2001) found most populations were distinguishable, and genetic distance and geographical distance were significantly correlated, although they also noted clustering of populations based on climatic similarity rather than proximity. Interestingly, *N. pulchra* individuals were homozygous, indicating very high rates of self-pollination, which reduces genetic variation within populations but increases it among populations. The native annual grass *Vulpia microstachys* is also highly self-fertilizing but exhibits within- and between-population allozyme variability similar to outcrossing species, perhaps due to sporadic bursts of outcrossing (Adams and Allard 1982). Knapp and Rice (1996) analyzed allozyme variation in 20 populations of *Elymus glaucus*: variation at the species level was very high and populations clearly differentiated, but within-population variation was lower, probably resulting from selfing and patchy distribution of populations. Their results were confirmed in another study of *E. glaucus* (Wilson et al. 2001), which further reported that genetic distance between populations could not be predicted from geographical distance, serpentine substrate, or habitat moisture; only two genetic clusters emerged, based on elevation.

Two studies of *Nassella pulchra* populations evaluated both quantitative traits and genetic material to develop information about the spatial scale at which germplasm transfer between sites is suitable. Dyer and Rice (1997b) investigated the genetic structure within a single population that occurs on two intermixed microhabitats (mound and intermound topography) at Jepson Prairie. The common garden experiment revealed phenological differences between mound and intermound plants; however, DNA analysis of the whole population did not show any corresponding genetic differentiation. When the DNA data were examined at a spatial scale below that of the whole population, genetic structure related to microhabitat differences emerged. At a much larger scale, Knapp and Rice (1998) sampled 10 populations across the state. Populations were strongly differentiated for isozymes and for quantitative traits, but each data type gave different population groupings. Quantitative trait variation (coastal vs. interior) was strongly correlated with climate, whereas isozyme variation (north vs. south) was associated with geographical distance between populations. Knapp and Rice (1998) concluded that because their study suggests quantitative traits are likely better indicators of local adaptation than isozymes, recommendations about the spatial scale of seed translocation should be based on quantitative traits, or on a climatic proxy.

Restoration

The goal of restoration of Central Valley grasslands is to reintroduce native perennial grasses and/or to increase the abundance of native species in general. Many of the academic studies described in this chapter that focused on native species (see, e.g., sections on competition, fire, grazing) were undertaken with the explicit goal of producing results applicable to restoring California's grasslands. Another valuable source of grasslands restoration information is the California Native Grasslands Association (2005), which aims to "develop, promote, preserve, and restore native grasses and grassland ecosystems in California" in part by encouraging all interested parties to exchange ideas, research, and practical knowledge in conferences and through its journal *Grasslands*.

Starting in the early 1990s, the commercial production of native grass seed created the ability to plant large acreages (Stromberg and Kephart 1996). Very little was known at the time about the cultural practices needed to successfully establish most native grasses on a large scale. At this writing the state of the knowledge is: native perennial grasses have seedlings that develop slowly, remaining at a small stature through the first year of growth. This means that competition from rapidly growing annual grasses is severe. Management that reduces nonnative annual grasses must be ongoing for the first 2 to 3 years following planting of the native perennial grasses (Anderson 1993; Stromberg and Kephart 1996). Best results for initial establishment occur when weed control begins the year prior to planting. Introduction

of native forb species into the restoration mix is only now being tested in the field (Carlsen, Menke, and Pavlik 2000; Brown and Bugg 2001).

On upland or rangeland sites characterized by well-drained soils, the following species of grasses are currently sold commercially and used extensively in restoration plantings: *Nassella pulchra*, *N. cernua*, *Poa secunda*, *Elymus glaucus*, *E. multisetus*, *Melica californica*, and *Hordeum brachyantherum*. On bottomland, flood-prone sites with fine-textured soils the following species have grown well: *Leymus triticoides*, *H. brachyantherum*, *N. pulchra* (flood-tolerant collection), *E. glaucus*, and *E. trachycaulus*. Planted native perennial grass stands have become increasingly common over the past several decades. Many of these stands are dominated by large, well-established individuals. What will be their fate as they interact with the local livestock grazing? How should the bottomland restoration sites be managed? What should be the ultimate target association?

Areas for Future Research

The knowledge base from research and management in the Valley Grassland has increased remarkably since publication of the previous editions of *TVC*. Much remains to be done, and several of the items below remain from the list of Heady (1977).

1. Further study on more sites is required to understand better the spatial and temporal variation of grassland species in relation to climate and management.
2. The taxonomy and population dynamics of decomposers need attention.
3. More experiments on competition between annual and perennial herbaceous plants would help to better define potential for natural and managed recovery of natives.
4. The relative impacts of many kinds of grazing animals remain almost unknown.
5. Seed population dynamics in relation to grazing and climate needs more work.
6. Wetland and saltbush variations of this type still have not been adequately mapped, described, or studied in either their original or their present conditions.
7. On the practical side, measurement of pollution impacts and climate change on Valley Grassland would help to define the future of much land in the Central Valley.
8. Little reliable information exists about response to specialized livestock grazing systems or the effectiveness of grazing for fuel management.
9. Much plant genetic work needs to be done.
10. More work is needed on native annuals.
11. Further research is needed on species composition, dominants, and extent of California's pre-European settlement grassland.

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