



TWENTY-THREE

Grasslands

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Introduction

Much of California's original grassland habitat has been lost to both changes in hydrology and in urban and agricultural development. Even with this extensive habitat loss, more than 10% of California's land area remains covered by grasslands today (Corbin et al. 2007a, Barbour et al. 2007). These remaining grasslands are among California's most altered ecosystems (Corbin et al. 2007a, Jantz et al. 2007). Non-native plant species comprise more than 90% of plant cover in most grassland areas, with many sites below 1% native cover (Bartolome et al. 2007). Even in their non-native dominated state, California's grasslands are a tremendous diversity hotspot, averaging more than fifty plant species per 30 x 30 meter area (Heady et al. 1992) and providing habitat for nearly 90% of state-listed rare and endangered species (Skinner and Pavlik 1994) and seventy-five federally listed plants and animals (Jantz et al. 2007).

These grasslands provide many ecosystem services critical for adjacent agricultural and suburban/urban areas. Almost all of California's surface water passes through grasslands and oak woodlands (Tate et al. 1999). The grasslands provide high INFILTRATION rates that attenuate storm events, leading to gradual release of storm water to streams (Lewis 1968,

Dahlgren et al. 2001). This reduces flood risk while also maintaining streamflow into the dry season. Grasslands can also improve water quality by filtering pathogens, nutrients, and sediments, serving as effective buffer strips between agricultural and urban uplands and streams (Tate et al. 2006, Atwill et al. 2006). California's grasslands contribute significantly to regional carbon storage through their large spatial extent and high quantity of carbon storage per unit area (Silver et al. 2010). Grasslands also support many of the pollinators needed in California's crop systems (Chaplin-Kramer et al. 2011). Direct economic benefits of these grasslands include their provisioning of 75% of the state's livestock forage (Corbin et al. 2007a, CCCC 2009, Cheatum et al. 2011). Because 88% of California grasslands are privately owned (Jantz et al. 2007), their conservation and restoration depend largely on private land owners and the ways they balance management for livestock production, biotic diversity, and ecosystem services (SRDC 2006, Barry et al. 2006, FRAP 2010, Ferranto et al. 2011).

Managing California's grasslands can be challenging because their structure and function are influenced by multiple, interacting controllers. This produces heterogeneous

community and ecosystem dynamics across space and time (Huenneke and Mooney 1989). Grasslands are distributed across a broad range of precipitation regimes; from the high-rainfall coasts to drier inland valleys (Figure 23.1). Grassland structure and function vary across this precipitation gradient and with high temporal variability in weather across seasons and years (see Chapter 2, “Climate”). While precipitation patterns are the strongest controller of California grassland dynamics, within the confines of weather patterns grassland structure and function also respond to human management and interactions with soil type, topography, non-native plants, small mammals, insects, microbes, livestock, wild herbivores, and disturbance regimes (Figure 23.2) (Bartolome et al. 2007).

California’s Mediterranean climate makes its grasslands distinct from other North American grasslands, which are exposed to a temperate climate where temperature drives the seasonality of plant growth (Corbin et al. 2007b). In contrast, seasonality of precipitation largely governs ecosystem processes in California’s Mediterranean climate, with most plant production occurring during the cool, wet winters and with little plant activity during the hot, dry summers (Corbin et al. 2007b). California’s grasslands differ from other Mediterranean grasslands across the globe because of the stable long-term dominance of annual species in most areas of California. While annual species play an important role in other Mediterranean grasslands shortly after disturbances, successional dynamics eventually lead to domination by perennial species (Rice 1989). Domination of annuals likely makes California’s grasslands more sensitive to fluctuations in abiotic and biotic controllers and is likely the reason behind the need for persistent management to meet many conservation and production goals (Bartolome et al. 2007, Malmstrom et al. 2009).

California’s grasslands are experiencing further changes due to shifts in management and the environment, including nitrogen deposition, altered weather patterns, non-native species introductions, and altered grazing and fire regimes. California’s grasslands are also threatened by further land use change. Successful management of these grasslands, particularly in a changing environment, will require site- and region-specific approaches (Bartolome et al. 2007) because sites from different climate regimes and soil types respond differently to weather variability (George et al. 1988) and management (Bartolome et al. 2007).

Primary Factors Controlling the Distribution of California’s Grasslands

California’s 5,640,400 hectares of grassland (Bartolome et al. 2007) are most commonly found in well-drained areas below 1,200 meter elevation (Heady 1977), across a wide diversity of soils (Jackson et al. 2007) and across a broad precipitation gradient ranging from 12 to 200 centimeters per year (Bartolome et al. 2007). Many of the herbaceous species that dominate open grasslands are also key components of other California ecosystems (Bartolome et al. 2007), including oak savannas (Chapter 25, “Oak Woodlands”), shrublands (Chapters

22, “Coastal Sage Scrub,” and 24, “Chaparral”) and deserts (Chapter 30, “Deserts”). California’s grasslands experience a Mediterranean climate with a mismatch in the timing of ideal temperature versus moisture conditions for plant growth (Figure 23.3). Moisture limits plant growth in the hot and dry summers, while temperature and light limit growth during the cool, wet winters. Ideal periods for plant growth are thus restricted to short periods in the fall and spring (Evans and Young 1989, Bartolome et al. 2007). The growing season begins with the first significant rains (greater than 1.5 centimeters within a week) (Chiariello 1989) and continues until soil moisture declines in the spring (exact timing depends on amount and timing of precipitation as well as the water-holding capacity of soil).

When the system dries in the spring, most early- to mid-PHENOLOGY annuals set seed and SENESCE, avoiding the hot, dry summer conditions. Some summer annual species (e.g., tarweeds [*Hemizonia*, *Madia*] and wild lettuce [*Lactuca*]) do grow through the hot, dry summer, using their deep taproots to access moisture (Chiariello 1989, Bartolome et al. 2007). Native perennial grasses often begin growth early in the fall, sometimes even before the rains begin, and can grow later into the summer than most annuals. However, most native perennial grasses do experience aboveground senescence in the summer (Bartolome et al. 2007). This highly seasonal climate, with soil moisture limiting plant growth for four to eight months out of the year (Bartolome et al. 2007), results in stable grasslands even at total annual precipitation levels that, if evenly distributed through the year, would support woody-dominated species in temperate climates. In areas with precipitation patterns that can support either herbaceous or woody species, soils that are fine-textured tend to be dominated by grasslands (Tyler et al. 2007). While environmental conditions shape the distribution of many grasslands, some of California’s grasslands were formerly woody-dominated and were converted through burning, cutting, and herbicide applications (Tyler et al. 2007). The distribution of grasslands across broad precipitation gradients and soils leads to three key subtypes: interior, coastal, and more localized soil-specific grasslands (Keeler-Wolf et al. 2007) (Figure 23.4).

Interior Grassland

The most widespread grassland type is interior grassland (also known as valley grassland, south coastal grassland) (see Figure 23.4a). Interior grasslands tend to be distributed in the Central Valley as well as up to 700 meters into the foothills and coastal hills (particularly in the South Coastal hills and in the interior valleys of the Northern Coast Range) (Keeler-Wolf et al. 2007). Since the early nineteenth century, non-native grasses and FORBS have dominated these grasslands (Keeler-Wolf et al. 2007). Grass cover dominates, but forb species richness is four times greater than grass richness (Sims and Risser 2000). Some native perennial grasses persist in this system (e.g., purple needle grass [*Stipa pulchra*], valley wild rye [*Elymus triticoides*], blue wild rye [*Elymus glaucus*], and California brome [*Bromus carinatus*]), but their growth, survival, and seed establishment are limited in the interior grasslands by the fast growth, high density, shading effect, and high water use of the highly competitive non-native species (Corbin et al. 2007a). Interior grasslands extend across a wide mean annual precipitation gradient, producing variations in plant

Photo on previous page: California wildflowers in bloom at the North Table Mountain Ecological Reserve, Butte County. Photo: Valerie Eviner.



FIGURE 23.1 Distribution of grasslands in California. Additional grassland not shown here occurs in the understory of oak savannas and woodlands in much of the state (see Chapter 25, "Oak Woodlands"). Data from U.S. Geological Survey, Gap Analysis Program (GAP). Map: P. Welch, Center for Integrated Spatial Research (CISR).

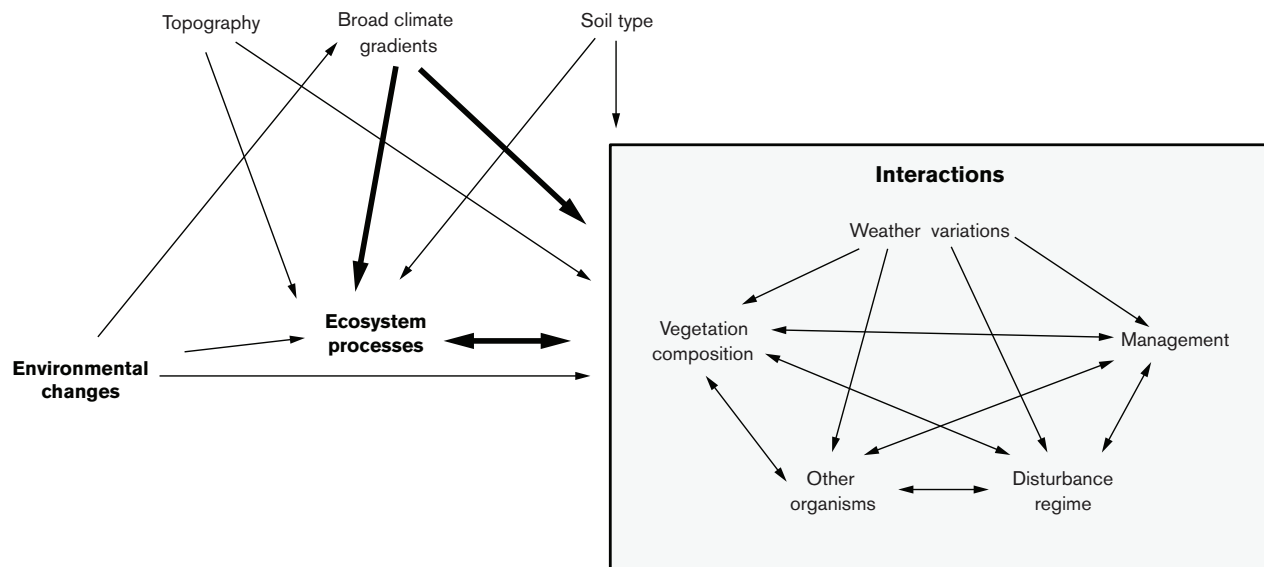


FIGURE 23.2 Controls over the structure and function of California's grasslands. Broad climate gradients are the primary controller of structure and function, while soil type and topography have impacts within the confines of climate conditions. All three of these state factors affect how weather variations influence interactions among vegetation composition, other organisms (e.g., small mammals, large herbivores, microbes, insects), disturbance regimes, and human management. These interactions determine ecosystem processes (C cycling, N cycling, water dynamics), which feed back to affect these interactive factors. Environmental changes (e.g., climate change, nitrogen deposition) can lead to unique interactions that influence grassland structure and function. Illustration by Valerie Eviner.

community composition. Species such as foxtail brome (*Bromus madritensis*) and red-stemmed filaree (*Erodium cicutarium*), both exotic, tend to be common in dry sites (less than 25 centimeter mean annual precipitation), while exotic species such as soft chess (*Bromus hordeaceus*), wild oats (*Avena barbata*), and broad leaf filaree (*Erodium botrys*) tend to be more common on wetter sites (65–100 centimeter mean annual precipitation) (Bartolome et al. 1980).

Coastal Grassland

Grasslands (also called prairies) along California's central and north coasts (ranging from San Luis Obispo to southern Oregon) tend to experience longer, wetter growing seasons than inland areas (Ford and Hayes 2007, Keeler-Wolf et al. 2007) (see Figure 23.4b). In addition, fog inputs mitigate summer moisture limitation and can account for 28% to 66% of root water uptake by perennial grasses in summer (Corbin et al. 2005). These wetter conditions (especially when precipitation is greater than 100 centimeters per year) lead to dominance by native and non-native perennial herbaceous and woody species. Common woody invaders include Scotch broom (*Cytisus scopartus*), French broom (*Genista monspessulana*), and gorse (*Ulex europeus*) (Heady et al. 1992, Ford and Hayes 2007). Overall, native cover is higher in coastal than interior grasslands. The annual non-natives that are common in the interior grasslands are often only minor components of the coastal grasslands or restricted to disturbed areas (Corbin et al. 2007a). While some of these coastal grasslands are stable as grasslands, particularly in the drier sites, others are maintained by disturbance regimes such as burning, live-stock grazing, and deer browsing that impede the persistence of woody plants (Ford and Hayes 2007).

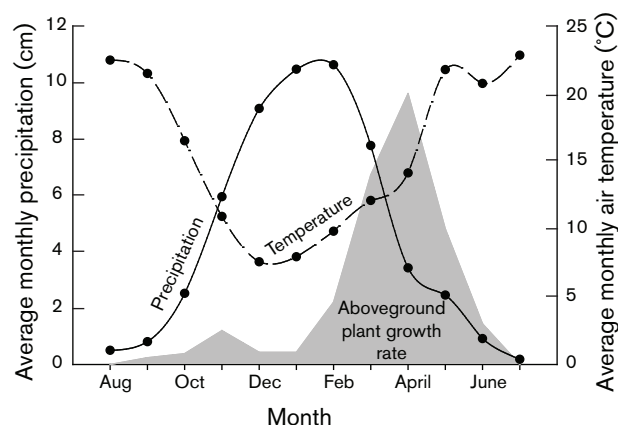


FIGURE 23.3 Seasonal variations in temperature (dashed line) and precipitation (solid line) drive plant growth rate (gray shaded area), with most production occurring when both moisture and ideal growing temperatures are present. Temperature and moisture data are from the California Irrigation Management Information System (CIMIS), averaged across 1985 through 2005 and across grassland sites, including: Sierra Foothills, San Joaquin Valley, Bay Area, Sacramento Valley, North Coast Valley, South Coast Valley, and Central Coast Valley. The left-side y-axis provides the precipitation scale, while the right-side y-axis represents the temperature scale. Aboveground growth rate is not present on either y-axis, but scales from 0 to 200 g/m²/month. Growth rate data is a seasonal average across experimental sites in the Central Valley and North Coast (Eviner, unpublished data). Source: Figure updated from Biswell 1956.

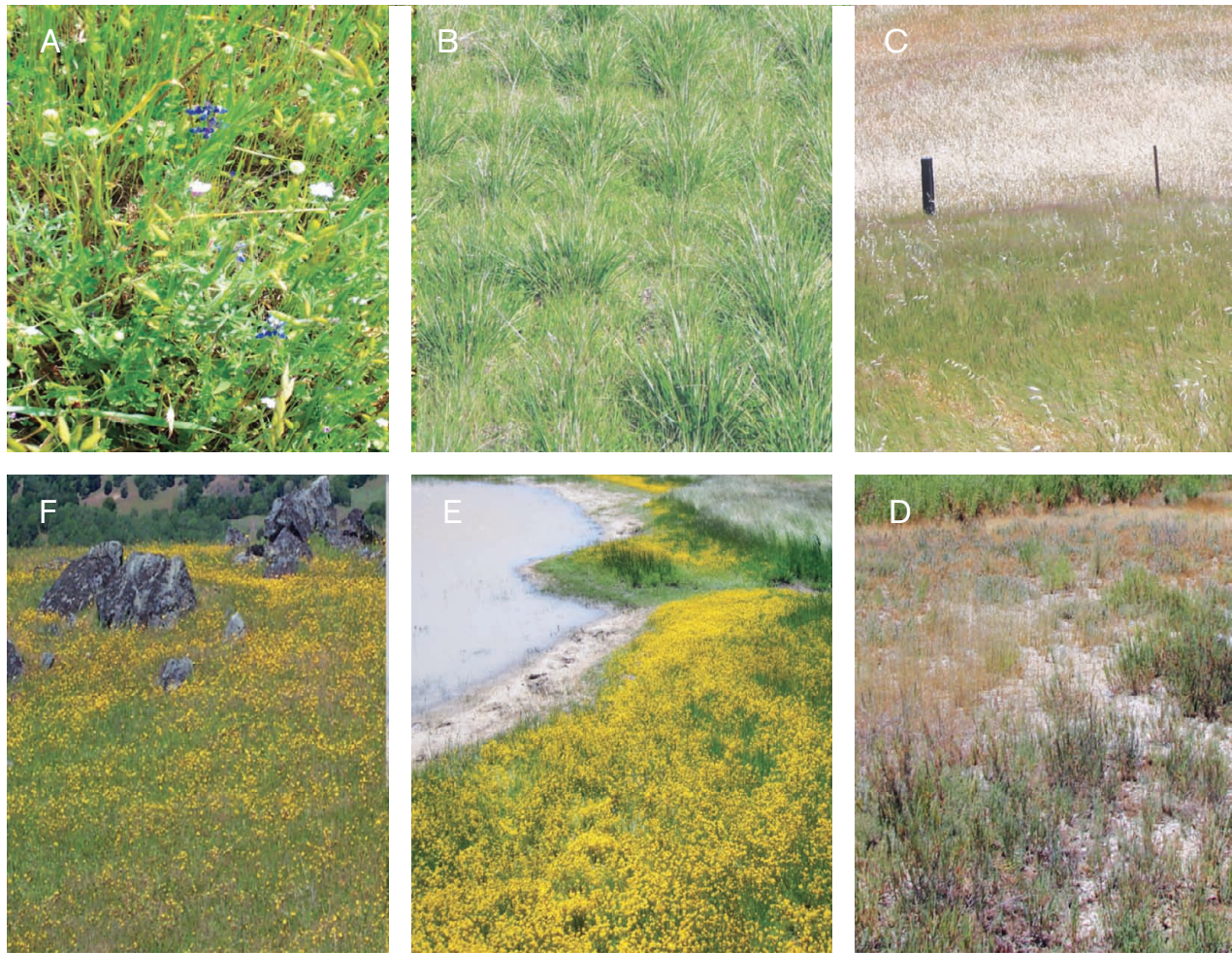


FIGURE 23.4 Diversity of California grassland types. Photos: Valerie Eviner.

- A Annual grassland with a mix of grasses, forbs, and legumes (Interior Coast Range, Mendocino County).
- B Native perennial grassland (Coast Range, Marin County).
- C More recent invasion of late-season non-native grasses (goatgrass, medusa head) in the foreground (green), invading into naturalized annual non-native grassland (background, senesced) (Interior Coast Range, Mendocino County).
- D Alkali grassland (Sacramento Valley floor, Glenn County).
- E Vernal pool (Sacramento Valley floor, Solano County).
- F Serpentine grassland (Interior Coast Range, Mendocino County).

Subtypes of Grasslands Determined by Unique Soils

Unique soil conditions in both interior and coastal grasslands create relatively small patches of distinctive grassland types, including serpentine, alkali sinks, and vernal pools. Serpentine soils are derived from rock from the earth's mantle. They tend to be nutrient-poor, with low calcium to magnesium ratios, high levels of heavy metals (particularly nickel), and low water availability. These stressful soil conditions lead to a low-productivity system with sparse, short plants and a high degree of endemism (species that are unique to particular locations). Serpentine sites are usually dominated by diverse native forbs, with less than 10% grass cover (see Figure 23.4f). While serpentine grasslands typically have far fewer non-native species than surrounding grasslands on nonserpentine

soils, invasion from surrounding grasslands does occur, particularly in areas receiving high amounts of nitrogen deposition (Harrison and Viers 2007).

Vernal pools are shallow, seasonal wetlands within a grassland matrix, usually found in shallow depressions with an impermeable soil layer (see Figure 23.4e). While the edges of vernal pools may be dominated by upland grassland species, the pools themselves contain a rich diversity of native and introduced grasses and forbs with composition strongly influenced by depth and duration of flooding (Solomeshch et al. 2007). Alkali sinks (see Figure 23.4d) are also seasonal wetlands but with a high pH and high salinity. These foster a rich community of native and introduced grasses and forbs including a number of endemic, threatened, and endangered plants (Heady 1977, Dawson et al. 2007).

Variations within Grassland Types: Local Controls over Structure and Function

While broad precipitation gradients and soil types can determine the distribution of distinct grassland types, each grassland type also contains considerable spatial and temporal variation within it. Interactions of multiple biotic and abiotic controllers mediate heterogeneity in community and ecosystem dynamics (Huenneke and Mooney 1989) (see Figure 23.1), as described in the following sections.

TOPOGRAPHY AND SOILS

California's grasslands occur on diverse soil types, including five of the twelve SOIL ORDERS. Even at a local scale, soil can be highly heterogeneous, affecting vegetation composition and growth through differences in soil fertility and water infiltration and storage (Jackson et al. 2007). Species such as soft chess are common on many soil types, but soil type limits the distribution of many other species, including wild oats, medusa head (*Taeniatherum caput-medusae*), and filaree (Evans and Young 1989). Clay soils have higher water-holding capacity and thus tend to increase plant production. Similarly, deep soils increase plant production by providing water to deep-rooted plants (Reever Morghan et al. 2007). Other soil characteristics, such as pH, nutrient content, soil organic matter and texture, can also influence community composition (Hoopes and Hall 2002).

Topography also has strong impacts on local heterogeneity in vegetation composition and production, largely through its impacts on microenvironment (McNaughton 1968, Evans and Young 1989, Heady et al. 1992). For example, south-facing slopes are so much drier and hotter than north-facing slopes that the growing season can be one month shorter on south-facing slopes (Hufstader 1978). North-facing slopes tend to favor species with deeper roots, greater water use and later phenology (Ng and Miller 1980). Thus native perennials and late-season invaders such as goatgrass (*Aegilops triuncialis*) are more common on north-facing than south-facing slopes (personal observation). Germination rates tend to be higher on north-facing slopes (Evans et al. 1975), but it is not clear whether this is due to environmental conditions at germination or variation in seed characteristics determined by environmental conditions during seed production the previous spring. Topography can also alter the impacts of grazing (Huntsinger et al. 2007) and elevation (Bartolome et al. 2007) on community and ecosystem dynamics.

VARIATIONS IN WEATHER

As discussed previously, the amount and seasonality of moisture and temperature determine the presence of grasslands, while precipitation gradients structure the distribution of grassland types. Variations in grassland structure and function within a given site are strongly driven by fluctuations in weather patterns within a growing season and across years (Heady et al. 1992, Bartolome et al. 2007, Keeler-Wolf et al. 2007). At a given site, annual precipitation can vary as much as 50 centimeters to 100 centimeters from its long-term mean (Pitt and Heady 1978, Reeve Morghan et al. 2007), with high variation particularly associated with El Niño–Southern Oscillation events (Reeve Morghan et al. 2007). Lower rain-

fall years tend to produce lower plant diversity (Bartolome et al. 1980), but total rainfall does not reliably predict plant production and community composition—the timing of rainfall is far more important than the annual total (Figure 23.5) (Pitt and Heady 1978, George et al. 2001, Reeve Morghan et al. 2007, Suttle et al. 2007).

Early fall weather conditions can have large impacts on vegetation composition, mediated through plant germination characteristics. The timing and temperature of initial fall rains can influence the germination of rare plants (Levine et al. 2011) as well as the identity of dominant plants (Pitt and Heady 1979). Alternating dominance among grasses, forbs, and legumes has been frequently observed across years in California's grasslands (Pitt and Heady 1979, Keeler-Wolf et al. 2007) and has been attributed to variations in weather conditions. An initial flush of germinating rains (at least 1.5 centimeters with a week) stimulates rapid germination of the annual grasses, depleting most of their seedbank (Young and Evans 1989, Chiariello et al. 1989, Bartolome et al. 2007). If precipitation continues throughout the fall, grasses dominate the vegetation throughout the growing season. However, when a germinating rain is followed by a dry fall, the germinated grasses are likely to die. In these years grasslands are dominated by forbs (e.g., filaree) that can survive the fall drought or forbs and legumes that germinate with later rains (Young and Evans 1989, Bartolome et al. 2007, Keeler-Wolf et al. 2007). The response of vegetation composition to rainfall patterns can vary greatly across sites, so that the conditions for a “forb year” are likely to result in more frequent patches of forbs across the landscape, among diverse vegetation patches (Jackson and Bartolome 2002).

Precipitation patterns in the winter and spring also affect community dynamics. Extended winter or spring drought enhances clovers (*Castilleja*, *Medicago*, *Melilotus*, *Orthocarpus*, *Trifolium*) (Corbin et al. 2007a) and alters seed production (Ewing and Menke 1983). Midwinter droughts are common in California's grasslands, averaging nineteen days without rain in December through January (Reeve Morghan et al. 2007). These midwinter droughts favor perennials over annuals, which are less tolerant of dry conditions during the growing season (Corbin et al. 2007a). Spring precipitation strongly impacts the amount and timing of seed production, but the effects vary by species and ecotype. For example, during dry springs some species flower earlier while others have a later but shorter flowering period (Chiariello 1989). Late-spring and early summer rains can enhance the growth and fecundity of late-season species, such as the non-native yellow starthistle (*Centaurea solstitialis*) and native tarweeds. These late-spring rains are unlikely to affect most annual grasses (Pitt and Heady 1978), which are hard-wired to senesce by early summer even in the presence of ample moisture (Jackson and Roy 1986, Chiariello 1989). However, later-season noxious annual grasses, such as medusa head and goatgrass, do benefit from late-season rains (Eviner, Rice and Malmstrom in prep.). In addition to shaping community composition, this temperature and moisture variability strongly regulates the amount and timing of net primary production (discussed later in the chapter, under “Ecosystem Functioning”).

FIRE

Fire can have strong impacts on grassland structure and function, with effects depending on the timing, intensity, and fre-

quency of burning (D'Antonio et al. 2006). The effects of any individual fire are generally limited to less than three years (Bartolome et al. 2007) and include decreased soil moisture (Henry et al. 2006), increased soil available nitrogen and phosphorus, and increased rates of nitrogen mineralization and nitrogen fixation (D'Antonio et al. 2006, Reiner 2007). Fire also has short-term effects on soil microbial community composition, with decreased gram negative and positive bacteria (Docherty et al. 2012) and a slight decrease in extracellular enzyme activity (Gutknecht et al. 2010). Over the long term, frequent fires can decrease soil nitrogen and sulfur due to repeated volatilization losses (D'Antonio et al. 2006).

Impacts of fire on plant communities are varied (D'Antonio et al. 2006) and depend on the dominant vegetation prior to burns. Fires increase species richness of non-natives in areas dominated by non-natives before the burns and increase natives in native-dominated areas (Harrison et al. 2003). In general, fires increase the prevalence of forbs and legumes by removing thatch, thus increasing light and soil temperature. Sustained increases in forbs require annual burns, but particularly for native forbs, this is only true in ungrazed areas (D'Antonio et al. 2006). This is likely because grazing, like burning, removes thatch, thus increasing legumes and forbs. Spring burns favor native over non-native forbs, although the effects are weak and depend on burn frequency and grazing regimes (D'Antonio et al. 2006). Fires are often timed to control non-native species. For example, to control late-season noxious weeds such as medusa head and goatgrass, prescribed burns are targeted in the late spring, after most other annuals have senesced but before weed seeds have matured and dropped. The senesced annuals are dry enough to support a moderately intense fire, which can kill the seeds of late-season weeds. This can decrease weeds over the short-term but must be repeated to maintain weed control (Reiner 2007).

Fire regimes have been greatly altered by human activity. Native Americans frequently burned to enhance grassland production, alter grassland communities, and convert shrublands to grasslands (Bartolome et al. 2007). In the nineteenth century, fire frequency in the Central Coast was one to five years, but it now has decreased to twenty to thirty years (Greenlee and Langenheim 1980). Near urban areas, however, fire frequency has increased (Bartolome et al. 2007). These changes in fire regime have strong potential effects on ecosystem and community dynamics (D'Antonio et al. 2006, Bartolome et al. 2007).

Biota

Diverse biota rely on California's grasslands for habitat and actively shape grassland structure and function through their interactions (see Figure 23.1).

LARGE HERBIVORES

Herbivory is a critical controller of most of the world's grassland ecosystems, many of which have evolved under grazing pressure. The extent of adaptation to grazing in California's native flora is unclear. California's native grassland flora was exposed to grazing and browsing by the rich megafauna present during the Rancholabrean (150,000 years before present [YBP] to 11,700 YBP), including bison, elk, deer, mammoth, pronghorns, horses, and camels. (Edwards 2007). These mega-

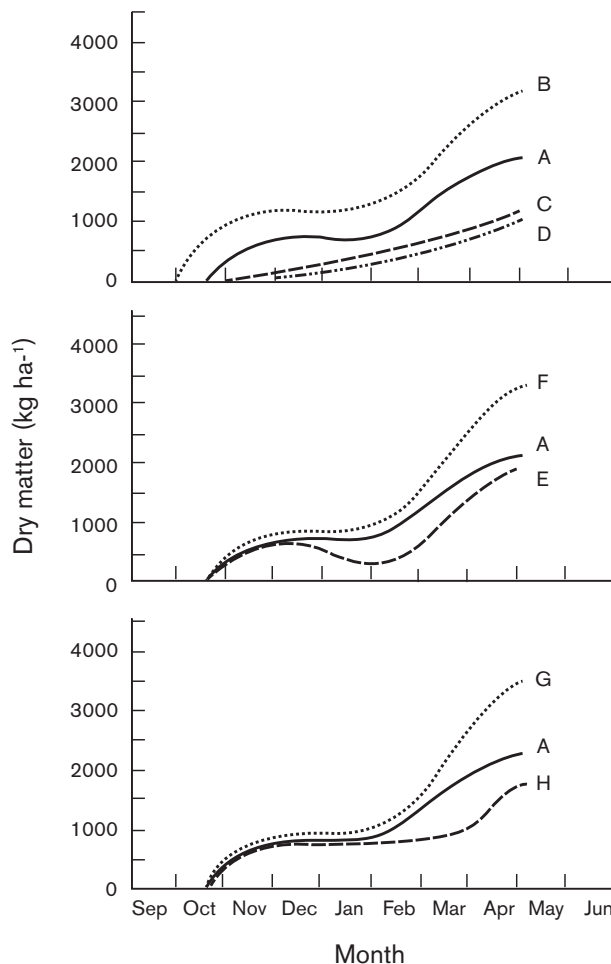


FIGURE 23.5 Seasonal forage production, as affected by seasonal weather patterns, at the San Joaquin Experimental Station (data from 1935 through 1984). Curves are associated with the following weather conditions: (A) average fall, winter and spring; (B) warm, wet fall, average winter and spring; (C) cold, wet fall, average winter and spring; (D) dry fall, average winter and spring; (E) average fall, cold winter, average spring; (F) average fall, mild winter, average spring; (G) average fall, short winter, early onset of warm spring temperatures; (H) average fall, long winter, late onset of warm spring temperatures. Source: George et al. 2001.

fauna were largely absent during the Holocene (11,700 YBP to the present), leaving a significant time period when plants could have adapted to the absence of megafauna. Even in the absence of megafauna, California grasslands continued to experience high rates of herbivory by rodents, rabbits, hares, birds, and elk (Edwards 2007). While deer and pronghorn have been prevalent for part of the Holocene, they are mostly browsers, so their main effect is likely exclusion of woody species with more modest impacts on herbaceous community composition (Edwards 2007). Herbivore identity has large impacts on vegetation composition. Cows and horses preferentially consume grass, while sheep and deer preferentially consume forbs. Antelopes consume grasses, forbs, and shrubs, changing preference with season (Edwards 2007). Similarly, tule elk consume forbs in the spring and summer and consume grasses in the fall and winter (Johnson and Cushman 2007). Removing elk from coastal grasslands decreased annual plant cover and increased some non-native perennial grasses but did not affect other perennials (Johnson and Cushman 2007).

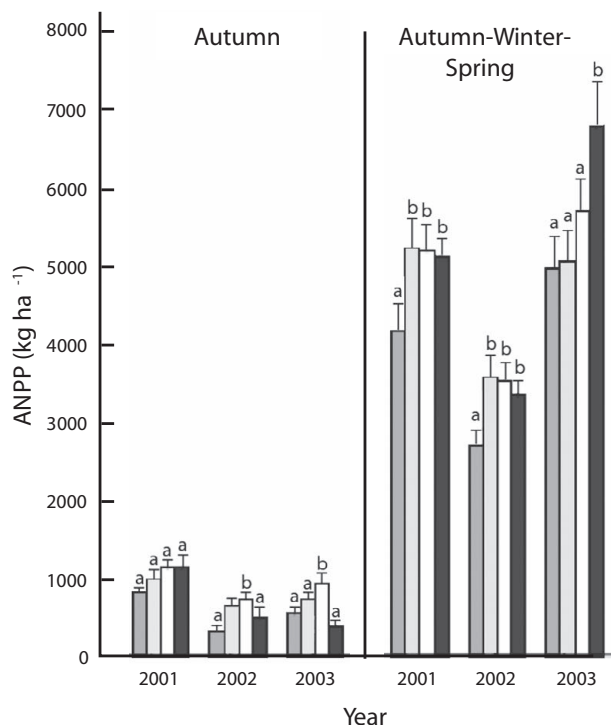


FIGURE 23.6 Effects of residual dry matter (RDM) on aboveground net primary production (ANPP) at Sierra Foothills Research and Extension Center from 2001 through 2003. From left to right within each year, gray bars are 225 kg/ha RDM, dotted bars are 560 kg/ha RDM, white bars are 900 kg/ha RDM, and black bars are 5,000 kg/ha RDM. Within each year, bars labeled with different lowercase letters differ significantly from each other. Source: Bartolome et al. 2007.

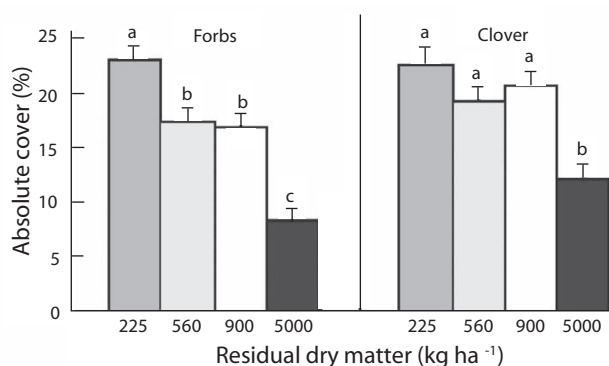


FIGURE 23.7 Impacts of residual dry matter (RDM) treatments on cover of forbs (left) and clovers (right) across five years at Sierra Foothills Research and Extension Center. Source: Bartolome et al. 2007.

Domesticated livestock have been significant controllers of California's grassland dynamics and economics since the 1770s on the coast and the 1820s inland (Jackson and Bartolome 2007; see Chapter 37, "Range Ecosystems"). While most livestock in California are cattle (approximately 5 million), they also include sheep (0.5 million), goats, pigs, and horses (Jackson and Bartolome 2007). Livestock impact grasslands in a number of ways. The first is consumption of live plant material. Precise timing of grazing has been used to control weeds, with livestock consuming the weedy species before it is able to produce viable seeds (Huntsinger et al. 2007).

A second mechanism driving grazing impacts is the accumulation of thatch or residual dry matter (RDM), the amount of senesced material remaining before the start of a new growing season (Bartolome et al. 2007). High RDM causes shading and lower temperatures, which can suppress new plants by decreasing seed germination and seedling growth (Figure 23.6, Autumn). Increasing RDM can decrease species richness, forbs, and legumes (Figure 23.7); and increase tall grasses such as wild oats and ripgut brome (*Bromus diandrus*) and other large-seeded species (Bartolome et al. 2007, Corbin et al. 2007a, Amatangelo et al. 2008). High RDM also decreases root to shoot allocation (Betts 2003), potentially affecting ecosystem processes such as erosion control, water dynamics, and carbon and nitrogen cycling. However, some amount of RDM benefits grasslands by increasing germination and production (see Figure 23.6) and controlling erosion (Bartolome et al. 2002, Corbin et al. 2007a). In sites with more than 38 centimeters of rainfall per year, RDM affects biomass production (Bartolome et al. 2002), with aboveground production generally highest at intermediate amounts of RDM (Amatangelo et al. 2008). The ideal amount of RDM varies by climate and topography, with higher RDM levels recommended at wetter sites and on steeper slopes (Bartolome et al. 2002). RDM levels are achieved through consumption of live plant tissue but also through consumption and trampling of senesced tissues, so early fall grazing can mitigate initially high RDM.

Grazing effects depend on livestock species as well as grazing timing, intensity, duration, and frequency (see Figure 23.1) (see Chapter 37, "Range Ecosystems"). Grazer impacts also vary through interactions with environmental conditions (climate, soil, elevation, slope/aspect, land use history) and initial plant community composition (Huntsinger et al. 2007). A meta-analysis of grazing impacts across diverse soils and precipitation conditions in California emphasized the context-dependent effects of grazing on plant communities (Stahlheber and D'Antonio 2013). For example, grazing effects on non-native forbs vary across a precipitation gradient (but could not be separated by interior versus coastal grasslands), strongly increasing non-native forb cover in dry sites and decreasing it at wetter sites. Grazing increased native forb cover in interior grasslands but reduced it in coastal grasslands (Stahlheber and D'Antonio 2013). Relative cover of non-native and native grasses more strongly reflects season of grazing and more weakly responds to site conditions. Wet-season grazing enhances native grasses (particularly at dry sites) while decreasing non-native grasses.

On average, grazing in California's grasslands increases non-native forb cover (but not richness), increases native forb richness (with little change in cover), increases non-native grass richness (with little change in cover), and increases native grass cover (Figure 23.8) (Stahlheber and D'Antonio 2013). The prevalence of case studies that contradict these trends, however, highlights the need for site-specific management guidance (see Chapter 37, "Range Ecosystems"). For example, in one coastal grassland, grazing increased native forb prevalence (Hayes and Holl 2003). In another case study, grazing decreased grass cover, increased forb cover, and had no effect on species richness and little effect on natives (Skaer et al. 2013). While grazing exclosures have been suggested as a tool to increase native vegetation, decades of livestock exclosure have inconsistent effects across sites (D'Antonio et al. 2006).

Grazing also alters soil properties. Moderate to high grazing (especially in the wet season) can increase soil BULK

DENSITY, which can in turn reduce water infiltration (Jackson and Bartolome 2007). Consumption of plant material can short-circuit the decomposition cycle, increasing the speed of nutrient release from plants and often concentrating nutrients in areas where animals congregate (e.g., under shade trees) (Jackson and Bartolome 2007). While the grazing effects on soil nutrients vary, grazing in California's grasslands generally increases soil nitrogen availability but decreases phosphorus and sulfur (Vaughn et al. 1986, Stromberg and Griffin 1996). Feral pigs, formerly domesticated livestock, can strongly influence grassland dynamics, especially as their populations increase rapidly. They disturb large soil areas at 5 to 15 centimeter depths in search of bulbs, roots, fungi, and invertebrates. This disturbance leads to short-term decreases in plant diversity and long-term increases in non-native plants and decreases in oak seedlings (Cushman 2007). Coastal studies have shown that native perennials can reestablish in pig exclosures, but also that pigs tend to avoid disturbing established native bunchgrasses (Cushman 2007). While feral pig disturbance can alter soil processes in other systems, effects on soil nutrient availability and cycling rates have not been shown in California's coastal grasslands (Cushman 2007).

SMALL MAMMALS

Small mammals are generally abundant in California's grasslands (Lidicker 1989), with varying population numbers and community dominance across sites and years (Pearson 1963, Lidicker 1989, Hobbs and Mooney 1985). Key small mammals include pocket gophers (*Thomomys bottae*), ground squirrels (*Spermophilus beecheyi*), mice (*Reithrodontomys megalotis*, *Peromyscus maniculatus*, *Mus musculus*), voles (*Microtus californicus*), moles (*Scapanus* spp.), rabbits (*Sylvilagus* spp., *Lepus californicus*), and in some regions kangaroo rats (*Dipodomys heermanni*) (Lidicker 1989, Schiffman 2007). Small mammals act as herbivores, granivores, and seed dispersers. Some species also cause significant soil disturbance (Schiffman 2007). Small mammals can reduce plant biomass through substantial herbivory and granivory (Bartolome et al. 2007). For example, in the San Joaquin Experimental Range, gophers, squirrels, and kangaroo rats consumed at least 33% of annual aboveground production (Fitch and Bentley 1949). In a grassland in the coastal hills, removal of small mammals increased aboveground biomass by 40% to 87%, partly by increasing grass abundance (Figure 23.9) (Peters 2007). During population peaks small mammals can consume up to 93% of the annual seed crop (Pearson 1964), and herbivory of live plants can decrease seed production by up to 70% (Batzli and Pitelka 1970).

Small mammals can strongly alter plant community composition (Hobbs and Mooney 1991, Bartolome et al. 2007, Cushman 2007, Keeler-Wolf 2007). Seed predation can range from 0% to 75% of seed production of preferred species (e.g., wild oats) (Marshall and Jain 1970, Borchert and Jain 1978), substantially shifting plant dominance. Density of preferred seed species can decline by 30% to 62%; the resulting competitive release can increase growth and fecundity of non-preferred plant species (Borchert and Jain 1978). Voles and mice decrease purple needle grass density, likely through granivory (Orrock et al. 2008). Similarly, squirrels and rabbits decrease purple needle grass establishment by 52%, recruitment by 30%, and reproduction by 43%. These effects are

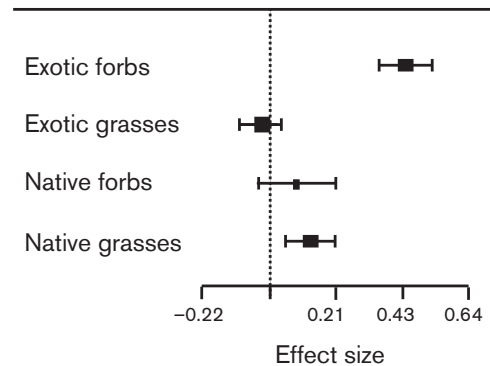


FIGURE 23.8 Effects of grazing on percentage of cover of exotic forbs, exotic grasses, native forbs, and native grasses, as determined by meta-analysis. Positive effect sizes indicate positive effects of grazing, and negative effect sizes indicate negative effects of grazing. Error bars indicate 95% confidence intervals. Source: Stahlheber and D'Antonio 2013.

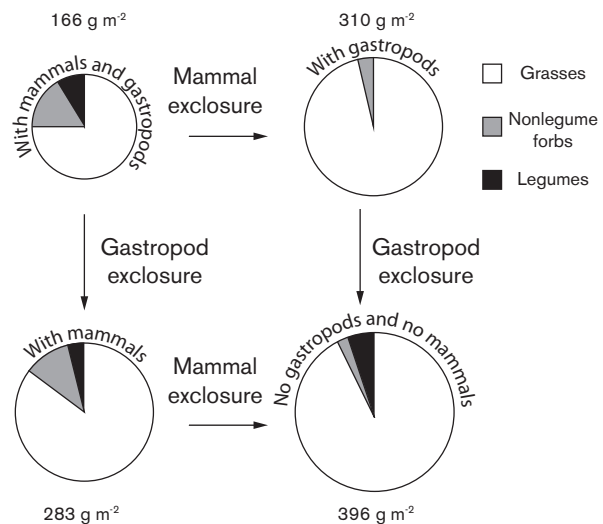


FIGURE 23.9 Effects of mammals and gastropods on aboveground biomass and composition during the 2001–2 growing season. Source: Peters 2007.

greatest when purple needle grass is located near patches of black mustard (*Brassica nigra*) (Orrock et al. 2008, Orrock and Witter 2010).

Pocket gopher populations can range from 26.6 to 100.8 ha⁻¹ (Lidicker 1989), with larger populations in ungrazed than grazed sites (Stromberg and Griffin 1996). Gophers consume approximately 8% of aboveground biomass (Lidicker 1989) and likely more belowground, since they specialize on roots and bulbs (Lidicker 1989). They preferentially feed on patches of legumes, forbs (Hunt 1992, Eviner and Chapin 2005), and geophytes (plants with storage organs that are underground) (Seabloom and Richards 2003, Schiffman 2007) when these are available. Despite these preferences, their diets often mirror dominant plant species composition such as annual non-native grasses and forbs (Hobbs and Mooney 1985, Schiffman 2007). Gophers disturb 1% to 30% of the soil surface each year, and on average any given soil surface turns over every three to fifteen years (Hobbs and Mooney 1985, Bartolome et al. 2007). Mounds are preferentially built in patches

with high SOIL SHEAR STRENGTH, usually in grass patches with high root surface area (Eviner and Chapin 2005). This soil disturbance can strongly alter the plant community, but which plant species colonize mounds can vary year to year (Hobbs and Mooney 1985). In general, gophers increase the prevalence of forbs (Tyler et al. 2007) and annual grasses while reducing perennial grasses (Bartolome et al. 2007).

Burrowing is also a significant activity of ground squirrels, kangaroo rats, mice, voles, and moles. This burrowing can increase plant diversity, especially of native forbs, and can increase prevalence of non-native species adapted to disturbance. Native perennial grasses often decrease (Schiffman 2007). Burrowing can reduce soil bulk density and increase soil temperatures and short-term pools of soil nitrogen (Eviner and Chapin 2005, Canals et al. 2003, Bartolome et al. 2007). Ground squirrel densities can range from 4.2 to 45.2 ha⁻¹ (Lidicker 1989) and tend to increase with livestock grazing (see Chapter 37, "Range Ecosystems"). Ground squirrels form extensive burrows (Bartolome et al. 2007). They directly consume 3–7% of net primary production and harvest (but do not consume) up to an additional 16.8% of standing biomass (Lidicker 1989). Their most important food items include several forbs (filaree, tarweed, buckwheat (*Eriogonum* spp.), popcorn flower (*Plagiobothrys* spp.), ripgut brome seeds, and acorns (Fitch 1948). Their extensive burrows provide habitat for burrowing owls and many other animals (Lidicker 1989).

Like ground squirrels, kangaroo rats also tend to increase in population size under grazed conditions (see Chapter 37, "Range Ecosystems"). Their burrows increase non-native annuals and decrease natives (Schiffman 1994), and they can cache high quantities of seeds (Lidicker 1989). Kangaroo rats remove up to 16% of standing biomass (Fitch and Bentley 1949), although much of this plant harvest is associated with building runways and nests and not direct consumption. They are primarily granivores (Schiffman 2007) and can consume up to 95% of their preferred seed species, red stemmed filaree (Soholt 1973).

Voles have dramatic population variation, with densities ranging from 0.25 to 1,110 ha⁻¹ (Lidicker 1989). Their densities tend to decline with increased grazing (Bartolome et al. 2007), and they can be absent from heavily grazed sites (Lidicker 1989). At high densities they can harvest 61.4% of grassland productivity (Lidicker 1989), resulting in 50% to 85% decreased cover of their preferred food species (wild oats, ripgut brome, Italian ryegrass [*Festuca perennis*]) and 70% decreased seed fall (Batzli and Pitelka 1970, Batzli and Pitelka 1971). Their activity can both increase (Fehmi and Bartolome 2002, Bartolome et al. 2007) and decrease (Lidicker 1989) plant species richness. Voles selectively feed on legumes, some grasses, and some forbs (e.g., filaree [Rice 1987], yarrow [*Achillea*], figwort [*Scrophularia*], wild lettuce, clover [*Medicago*], dock [*Rumex*]), and some of these species are absent from areas with vole activity (Lidicker 1989). Their selective granivory can alter plant community composition (Cockburn and Lidicker 1983), decreasing wild oats while increasing other annuals such as ripgut brome, Italian ryegrass, and foxtail barley (*Hordeum murinum*) (Borchert and Jain 1978).

Rabbits are abundant in California's grasslands and intensively use this system (Zedler and Black 1992). Like other small mammals, during population outbreaks they can consume great quantities of biomass and alter community composition (Vivrette and Muller 1977).

INSECTS, ANNELIDS, AND GASTROPODS

California's grasslands host a diverse and abundant insect fauna. Arthropod biomass has been measured at 126 g m⁻² belowground and 1.2g/m² aboveground (Burdic et al. 1979, Heady et al. 1992). The roles of many insects have not been studied in this system, but some are known to impact structure and function. Ants are seed consumers and dispersers. Most studies on their effects have taken place in serpentine grasslands, where they have a density of one ant mound per 100 m² with feeding paths 10–12 meters long (Hobbs and Mooney 1985). Some studies have shown that ant foraging alters the spatial distribution (Peters et al. 2005) and composition (Hobbs 1985) of plants (Hobbs 1985), but others studies have seen no impact of ant seed dispersal on plant communities (Brown and Human 1997). The selectivity of ants likely varies by year, with low selectivity in dry years with low food availability (Peters et al. 2005). Ant preference for certain plants also changes throughout the season as initially preferred plant seeds are consumed (Hobbs 1985). Ant mounds, though they make up a small area of grassland (approximately 0.6% [Hobbs 1985]), consistently have been found to increase legumes and non-native annual grasses (Peters et al. 2005), while decreasing forbs and enhancing seed production of other species (e.g., peppergrass [*Lepidium nitidum*]) (Brown and Human 1997). Ant mounds also increase soil bacteria, fungi, microarthropods, and nematodes (Boulton et al. 2003) as well as soil organic matter and nutrients such as phosphorus, potassium, and nitrogen (Beattie 1989, Boulton et al. 2003).

Grasshoppers in California's grasslands, though little studied, strongly affect vegetation composition and standing biomass in other grasslands, consuming as much as 25–92% of standing vegetation (Joern 1989). California hosts almost two hundred species of grasshoppers that feed on grasses and forbs, making it highly likely that they are key players in this system. In a native California perennial bunchgrass stand, grasshopper density averaged 2.3 m⁻² (June through August) with an annual consumption rate of 140 kg ha⁻¹, large enough to cause economic forage losses (Porter et al. 1996). Most grasshoppers in California reach maturity in late spring and summer, so they have little effect on annual grasses, which have largely senesced by this time (Porter et al. 1996, Joern 1989). Thus grasshoppers in California consume more native than non-native grasses, although their most abundant food item is forbs (Porter and Redak 1997). Care must be taken in generalizing the impacts of these few studies, since they focus on one grasshopper species, and different grasshopper species are frequently associated with different plant species (Stroehecker et al. 1968).

Gastropods (e.g., slugs, snails) can consume high amounts of aboveground biomass, and their exclusion can increase aboveground biomass 28–71% (see Figure 23.9) (Peters 2007). They strongly prefer certain plant species and can affect seedling survival (Peters et al. 2006, Strauss et al. 2009, Motheral and Orrock 2010). Their selectivity varies by season, with higher consumption of grasses in fall (leading to higher legume and forb cover) but higher forb consumption in winter (leading to higher grass cover). By spring, gastropod presence increases grass cover at the expense of forbs (Peters 2007). The impacts of gastropods on the plant community can be so great that their feeding behavior mediates about half of the changes in plant community composition seen in response to experimental global changes (Peters et al. 2006).

Earthworms are also important players in California's grasslands. Earthworms stimulate litter mass loss rates by breaking up litter and incorporating it into the soil. Earthworm burrowing and casting also increase water infiltration and aeration by increasing macropores (Standiford et al. 2013). Both native and non-native earthworms occur in California grasslands, with non-native earthworms dominating disturbed and fertile environments and natives dominating relatively undisturbed grasslands (Winsome et al. 2006). The non-native earthworms are more active than natives, leading to greater physical disturbance of the soil. Through this increased activity, non-native earthworms increase plant growth and uptake, enhance N turnover through litter decomposition, and decrease microbial biomass (Winsome 2003).

BIRDS

California's grasslands are primary habitat for some bird species and provide feeding and/or nesting grounds for other species. Their use can be seasonal or year-long (reviewed in Lidicker 1989, CPIF 2000, Shuford and Gardali 2008). While few studies document the ecological impacts of these birds on California's grasslands, there are some critical roles played by grassland birds in general. Birds can have substantial impacts on plant populations and species composition through seed dispersal and granivory, with effects that are distinct from those of granivorous small mammals (reviewed in Espeland et al. 2005). Many of the same bird species are also important insectivores, controlling populations of grasshoppers and other potential pest insects, and sometimes also disturbing soil to feed on insects, grubs, and worms (Fix and Bezener 2000, Sekercioglu 2006). Examples of birds in California's grasslands that are both granivores and insectivores include savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus sarnanum*), horned lark (*Eremophila alpestris*), western meadowlark (*Sturnella neglecta*), vesper sparrow (*Pooecetes gramineus*), and lark sparrow (*Chondestes grammacus*) (Lidicker 1989, Fix and Bezener 2000, see both references for a more extensive list). The relative importance of seeds versus insects in bird diets often vary by season and by species (Shuford and Gardali 2008). Many of these birds nest on the ground from early spring through July, so their breeding can be disrupted by mowing, grazing, disking, or burning during the spring (CPIF 2000). Their populations have been steadily declining, at least partly due to loss of continuous grassland habitat (CPIF 2000, Rao et al. 2008).

Predaceous birds can have significant effects on grassland structure and function through their controls over the populations of small mammals. In order to avoid predation, in the presence of birds, small mammals alter their behavior and habitat use, leading to less use of areas with short or sparse vegetation (Sekercioglu 2006). Most predatory birds also feed on smaller birds, amphibians, reptiles, large insects, and sometimes carrion (Fix and Bezener 2000). Key avian predators in California's grassland include hawks (red-tailed [*Buteo jamaicensis*], ferruginous [*Buteo regalis*], Swainson's [*Buteo swainsoni*], northern harrier [*Circus cyaneus*]), owls (burrowing [*Athene cucularia*], short-eared [*Asio flammeus*]), and the white-tailed kite (*Elanus leucurus*) (Lidicker 1989, CPIF 2000, Shuford and Gardali 2008).

NONAVIAN PREDATORS

Since small mammals and insects can have such large effects on California grassland structure and function, regulation of these groups by predation has significant impacts on these grasslands (Schiffman 2007). Predatory animals are diverse, including birds, snakes, coyote (*Canis latrans*), fox (*Vulpes fulva*, *Urocyon cinereoargenteus*), badger (*Taxidea taxus*), alligator lizards (*Elgaria* spp.), and the domesticated/feral cats (*Felis domesticus*) (Lidicker 1989). These species can have diverse diets, including insects, birds, bird eggs, small mammals, and in some cases, one another (Fix and Bezener 2000, Jameson and Peeters 2004, Stebbins and McGinnis 2012). Important insectivores include the Pacific tree frog (*Pseudacris regilla*), tiger salamander (*Ambystoma* spp.), skinks (*Eumeces* spp.), and a variety of lizards (western fence lizard [*Sceloporus occidentalis*], coast horned lizard [*Phrynosoma blainvillii*]) (Stebbins and McGinnis 2012). Omnivores are also common, eating a wide variety of plant species and tissues, as well as insects, earthworms, amphibians, reptiles, and small mammals (e.g., skunk [*Mephitis mephitis*], raccoon [*Procyon lotor*]) (Lidicker 1989, Jameson and Peeters 2004).

As described earlier, the small mammals with the largest impacts on grasslands include ground squirrels, gophers, and voles. The primary predators of ground squirrels include raptors (e.g., red-tailed hawk) and the western rattlesnake (*Crotalus viridis*). White-tailed kites, gopher snakes (*Pituophis melanoleucus*), and garter snakes (*Thamnophis* sp.) are considered the most important predators of voles. Key predators of gophers include gopher snakes, western rattlesnake, red-tailed hawk, barn owl (*Tyto alba*), great-horned owl (*Bubo virginianus*), and coyote (Lidicker 1989).

MICROBES

California's grasslands have high soil microbial biomass and richness (Sanchez-Moreno et al. 2011), with a dynamic microbial community that changes in response to plant communities (Hawkes et al. 2005, Batten et al. 2006), temperature, and moisture (Waldrop and Firestone 2006). Microbial community shifts can have important effects on plant communities and ecosystem processes. Seasonal shifts in microbial communities due to temperature and moisture lead to shifts in the soil enzymes that mediate decomposition and nutrient cycling, with many enzymes peaking in the early spring and/or winter and least active in the summer (Waldrop and Firestone 2006). Dry conditions can decrease bacterial biomass and can decrease (Alster et al. 2013) or increase enzyme activity (Henry et al. 2005). Higher spring precipitation reduces the abundance and diversity of fungi and increases decomposition rates (Hawkes et al. 2011). Microbial communities can directly affect plant performance, altering plant growth rate and root-to-shoot allocation, with effects varying by plant species (Brandt et al. 2009). Plant communities also can shape microbial communities. For example, non-native grasses have increased the population size and altered the composition of the ammonium oxidizer community, leading to more than doubled rates of nitrification over native grass soils (Hawkes et al. 2005). Increased nitrification can have strong effects on plant nitrogen availability, nitrogen retention, and water quality.

Arbuscular mycorrhizae (AM) are fungal symbionts with plants, exchanging plant carbon for various resources includ-

ing nitrogen, phosphorus, and/or water. Most grassland plants are mutualistic with these fungi (Hopkins 1987, Harrison and Viers 2007), and the composition of the AM community can alter plant growth and seed production, nutrient uptake, root-to-shoot allocation, and drought stress tolerance (Allen and Allen 1990, Nelson and Allen 1993, Harrison and Viers 2007). AM also strongly enhance soil aggregate formation, which can affect carbon and nutrient dynamics, soil water infiltration and storage, and erosion control (Rillig et al. 2002). AM in California's grasslands play a particularly important role in plant phosphorus uptake. In the presence of AM, plant production is nitrogen-limited, but without the AM symbiosis, plants are limited by phosphorus (Grogan and Chapin 2000). AM hyphal networks can associate with many individual plants simultaneously, leading to transfers of phosphorus (and possibly other resources) among diverse plant species. For example, when radioactive phosphorus was added to a given plant, that phosphorus was transferred to 20% of the plant's close neighbors through the AM network (Chiariello et al. 1982). This AM network among plant species can influence dynamics between native and non-native plants. For example, in the presence of the AM community the non-native Napa star thistle (*Centaurea melitensis*) dominated over native purple needle grass. However, when AM biomass was reduced, the non-native plant was much less competitive (Callaway et al. 2003), suggesting that the AM network provided the non-native plant with resources from the native plants.

AM communities change in response to environmental conditions, with much change not in direct response to environmental changes but mediated through vegetation changes (Rillig et al. 1998). Because AM species have plant species-specific effects, vegetation-induced changes in AM community composition can alter plant competitive outcomes (Allen and Allen 1990). A number of studies have shown that the AM community differs under native and non-native plants (Hawkes et al. 2006, Nelson and Allen 1993, Vogelsang and Bever 2009), with non-native plants exerting stronger effects on AM than native plants do (Vogelsang and Bever 2009). Non-native plants alter not only the soil AM community but also that associated with native plants. For example, when wild oats and purple needle grass grow as neighbors, the AM associated with wild oats dominated purple needle grass roots but purple needle grass did not affect the AM on wild oat roots (Hausmann and Hawkes 2009). This effect was particularly strong when wild oats established before purple needle grass (Hausmann and Hawkes 2010). In another study non-natives and natives both grew best associated with their own AM communities (Vogelsang and Bever 2009). Finally, non-native plant effects on the AM community increased the seed production of non-native plants but not native plants (Nelson and Allen 1993).

Dynamics between non-native and native plant species can also be mediated by microbial and viral pathogens. Crown rust can decrease wild oats while increasing purple needle grass (Carsten et al. 2001). In contrast, barley yellow dwarf virus and cereal dwarf virus can negatively affect both native and non-native grasses, but they have a stronger negative effect on natives, particularly because the non-native annual grasses enhance transmission of the viruses to natives (Malmstrom 1998). When exposed to these viruses and to competition with non-native annuals, first-year survivorship of natives can be halved (Malmstrom et al. 2006), with other studies showing the viruses can decrease native sur-

vival 0–80% and fecundity 30–70% (Borer et al. 2007). Grazing can interact with these viruses, but overall impacts are not unclear, with studies showing that vertebrate herbivores can increase plant infection by viruses (Borer et al. 2009) but that survivorship of the infected plants can increase (Malmstrom et al. 2006). The soil food web is an important mediator of biogeochemical processes. While only a limited number of studies have addressed it in California's grasslands, we know that abundance and richness of groups such as protozoa and nematodes are high but vary greatly across sites, seasons, and years (Freckman et al. 1979, Heady et al. 1992, Sanchez-Moreno et al. 2011, Baty 2012). Processes such as litter decomposition are strongly controlled by the size and composition of the food web, which is in turn controlled by both resource availability and predation (Barstow 2011).

Interacting Factors: Transition of California's Grasslands to a Non-Native-Dominated State

Frequent interactions among biotic and abiotic factors determine the structure and function of California's grasslands (see Figure 23.1). For example, the effects of gopher mounds on plant composition differ with precipitation (Hobbs and Mooney 1991), as the effects of burning on plant communities vary with grazing regime (D'Antonio et al. 2006). The interplay of multiple factors is perhaps best demonstrated by a suite of hypotheses about the causes of non-native plant domination in California's grasslands.

The composition of California's grasslands at the time of European settlement is not well documented (Wigand et al. 2007); it is unclear whether the currently common native species were previous dominants or were historically unusual species able to survive changing conditions. There has been substantial debate about the pre-European composition of this system, with theories ranging from: (1) it was dominated by native perennial bunchgrasses interspersed with native forbs, and replacement by exotic annuals was due to overgrazing and drought; versus (2) it was dominated by wildflowers (both annual and perennial forbs), which declined due to the competitive nature of the newly introduced exotic grasses and forbs (reviewed in Minnich 2008). While there are strong advocates for both of these alternatives, it is generally accepted that native systems likely contained perennial bunchgrasses and forbs, rhizomatous grasses, and annual forbs and grasses, with different plant groups dominating different regions (Bartolome et al. 2007). Perennial grasses likely dominated wetter areas, such as those adjacent to the coast, the windward aspect of the coast range, and wetter areas of the Central Valley. Annual forbs likely were present in all of California's grasslands but dominated in drier areas, including the foothills, the interior coast ranges, and in the drier areas of the Central Valley (D'Antonio et al. 2007). The abundance of forbs on most sites were likely to annually vary from rare to abundant, depending on weather and disturbance regimes (Schiffman 2007). Using the term "grasslands" to describe this diverse group of communities can underplay the current and historical importance and prevalence of forbs, and many advocate returning to the term "prairie," which was historically used to describe these diverse systems in California (Holstein 2011).

While we can only speculate about the composition of historical plant communities, we know that non-native species replaced the dominant native vegetation during the 1700s

and 1800s (Bartolome et al. 2007, D'Antonio et al. 2007). Non-native species invasions occurred in a number of waves (Heady et al. 1992, D'Antonio et al. 2007, Bossard and Randall 2007, Minnich 2008). Species such as wild oats, filaree, and mustard (*Brassica*) were found in adobe bricks of early Spanish missions, indicating their prevalence even before the mid-1800s, when European settlements and livestock expanded. Bromes (*Bromus* spp.) and barleys/foxtails (*Hordeum* spp.) spread in the 1860s and 1870s. In the late 1800s hairgrass (*Aira*), foxtail brome, and Napa starthistle invaded. Species currently invading California's grasslands include barbed goatgrass, medusa head, and yellow starthistle (*Centaurea solstitialis*) (Heady et al. 1992, D'Antonio et al. 2006, D'Antonio et al. 2007, Keeler-Wolf et al. 2007) (see Figure 23.4c); coastal grasslands are also currently being invaded by non-native perennial grasses, including velvet grass (*Holcus lanatus*), tall fescue (*Festuca arundinacea*), Harding grass (*Phalaris aquatica*), and orchard grass (*Dactylis glomerata*) (Corbin and D'Antonio 2010). California's grasslands now contain four hundred non-native plant species (Bartolome et al. 2007), amounting to 37% of California's invasive flora—the largest of any ecosystem in the state (Bossard and Randall 2007).

A number of hypotheses, all with strong experimental support, address what caused the widespread invasion of non-native species. Most of these hypotheses focus on transition from native perennial bunchgrasses (Bartolome et al. 2007, D'Antonio et al. 2007), which will be the focus of the next discussion. In areas that were not dominated by native perennial grasses, other mechanisms (e.g., superior competitor ability of invaders) may have driven the transition from native to exotic domination (Minnich 2008). Many have argued that the domination of non-native species resulted primarily from the competitive superiority of non-natives due to their rapid early-season growth, drought tolerance, high seed production, and earlier seed establishment (Bartolome and Gemmill 1981, D'Antonio et al. 2007). However, competition on its own was likely not enough to drive such dramatic shifts from native perennial bunchgrasses. Well-established stands of native perennial bunchgrasses resist invasion. Even though newly established native grasses can be initially invaded by non-natives, in a number of cases natives persisted in these invaded patches and eventually suppressed non-native grasses (Corbin and D'Antonio 2004, D'Antonio et al. 2007, Eviner et al. 2013). Thus the extensive transition from native to non-native domination that took place likely also required a stressor that decreased the performance or cover of natives if the previous dominants were perennial grasses.

Drought and overgrazing are the most commonly hypothesized such stressors driving the native to non-native transition (D'Antonio et al. 2007). While native grasses might have evolved under seasonal grazing and browsing, in the 1700s they were exposed to heavy, year-round livestock grazing. This could have exceeded the grazing tolerance of natives, while Mediterranean non-natives could tolerate it (Bartolome et al. 2007, Hille Ris Lambers et al. 2010). Overgrazing also decreased productivity through erosion and loss of soil fertility (Allen-Diaz et al. 2007). Moreover, the native grassland plants had evolved under wetter, longer growing seasons (Dyer 2007), and were likely particularly hard hit by severe, multiyear droughts in 1850–1851 and 1862–1864. Annuals cope with the prolonged dry season by producing seeds at the onset of summer and dying. This strategy might have allowed them to establish under low-rainfall conditions and to be poised to spread when the droughts ended (Reever Morghan et al. 2007).

In addition to drought and overgrazing, a number of other well-supported mechanisms might have contributed to invasion by non-native species. Increased settlement by Europeans across California wrought major changes to hydrology and fire regimes. River damming and levees destroyed many fertile, moist floodplains, decreasing the water and silt deposition that supported rich vegetation (Dyer 2007). Native Americans also managed grasslands through high-frequency burns, and the cessation of these burns may have increased non-natives (Dyer 2007, Bartolome et al. 2007). Another key land management change was the rise of crop agriculture, with extensive tilling that the native perennials could not survive (D'Antonio et al. 2007). In addition to land use changes, extensive biotic interactions could have contributed to the vegetation transition. In the late 1800s to early 1900s, increased hunting pressure on predators led to extremely high abundance of small mammals. Their extensive soil disturbance might have favored annuals, with their high seed production and ability to establish quickly on disturbed areas (Schiffman 2007). An already stressed native community could have been further decimated by grasshopper outbreaks. Because these outbreaks occur during summer, they would negatively affect perennials but have no effect on non-native annuals, which are already dead at this time of year (Joern 1989).

Once the transition to annual non-natives occurred, a number of mechanisms could have maintained the invaded state. Barley and cereal yellow dwarf viruses decrease native grass growth, survivorship, and fecundity (Malmstrom et al. 2005a, 2005b). The presence of non-native grasses more than doubles infection of native grasses by these viruses (Malmstrom et al. 2005a, 2005b), partly by increasing abundance of aphid—the vector of these pathogens (Borer et al. 2009). Non-native grasses also alter soil chemistry and microbial communities, which can feed back to favor non-natives over native plants (Grmn and Suding 2010, Hausmann and Hawkes 2010). Finally, the decline of native grasses might have caused widespread seed limitation, preventing natives from reestablishing on their own (Hamilton et al. 1999, Seabloom et al. 2003).

Ecosystem Functioning

This review of ecosystem function focuses mostly on the annual grassland, since it is the dominant type in California. As discussed earlier, in most of the world's grasslands dominance of annual species is limited to early successional stages. Most paradigms for understanding and managing grasslands thus focus on perennial grasslands. These frameworks are not adequate for understanding annual-dominated systems, where the annual growth habit, coupled with high interannual variability in precipitation, strongly influence functioning and management needs (Heady et al. 1992, Bartolome et al. 2007).

Net Primary Production (NPP)

Timing of plant production is driven by seasonality of temperature and moisture (see Figure 23.3), with an initial pulse of production early in the season when temperature and moisture are both ideal. When the first rains occur during colder periods, lower temperatures do not inhibit stand establishment but can limit growth (Evans and Young 1989). In

the winter, low temperatures inhibit aboveground biomass growth but root growth continues, reaching its peak before mid-March (Evans and Young 1989, Heady et al. 1992). When midwinter droughts occur, water can limit growth during the rainy season (Corbin et al. 2007a). As temperatures rise in mid- to late February, aboveground NPP increases, with peak biomass often occurring in mid-April to late May, just before the soil dries and plants begin to senesce (Evans and Young 1989, Heady et al. 1992).

The high variability in annual weather coupled with the annual growth form of the dominant plants renders NPP in California's grasslands extremely variable, with typical annual variations of at least 50% of mean NPP (Bartolome et al. 2007). For example, from 1935 through 1999 at the San Joaquin Experimental Range, aboveground NPP ranged from 1,008 to 5,040 kg ha⁻¹, while at Hopland Research and Extension Center, aboveground production ranged from 1,008 to 3,920 kg ha⁻¹ from 1953 through 1999 (George et al. 2001). Although California grasslands have been studied intensively for decades, limited ability persists to explain this variability in production using the conventional predictors of climate, soil type and residual dry matter (RDM) (George et al. 2001). NPP only weakly relates to total annual precipitation and is much more strongly affected by timing of rainfall during adequate temperatures for growth (see Figure 23.5) (Pitt and Heady 1978, George et al. 2001, Reeve Morghan et al. 2007, Suttle et al. 2007).

In general, NPP tends to be highest in years with high and steady rainfall in November through February (Murphy 1970, Pitt and Heady 1978, Reeve Morghan et al. 2007, Chou et al. 2008), particularly when temperatures are higher in this period (Pitt and Heady 1978, George et al. 2001). However, this generalization does not always hold—even in long-term datasets, the timing and total amount of precipitation do not always correlate with production (Pitt 1975, Duncan and Woodmansee 1975). Moreover, different sites respond uniquely to timing of rainfall. Sites in northern California's coastal range and foothills have their highest NPP when fall and winter are warm and wet. In contrast, a drier southern California site has its highest NPP in years with high spring precipitation (George et al. 2001). Plant community composition can strongly shape the impacts of spring rains on NPP. When vegetation at a site is dominated by species that senesce early to midspring, spring rains (March, April) either have no effect or decrease NPP (Pitt and Heady 1978, Reeve Morghan et al. 2007, Chou et al. 2008). However, late-season rains increase NPP at sites with late-season species, particularly in sites with summer annuals, which can produce up to 10% of a site's NPP. In these cases, the duration of the rainy season can determine the duration of the growing season (Hooper and Heady 1970, Chiariello 1989). In perennial-dominated grasslands along the coast, the duration of the growing season is also extended by moisture supplied through fog inputs (Corbin et al. 2005).

While weather conditions are likely the strongest controls over production (Corbin et al. 2007a, Bartolome et al. 2007), there are a number of other factors that also play an important role, within the constraints of weather patterns. When moisture is not limiting to growth, soil nutrients are the next-most limiting factor (Pitt and Heady 1979, Harpole et al. 2007). Nitrogen is the most commonly limiting nutrient to plant growth in this system, but NPP can also be limited by phosphorus or sulfur, depending on the site and the vegetation community. Some sites can respond equally to

nitrogen additions versus sulfur and phosphorus additions. Nitrogen additions will enhance grass production, while sulfur and phosphorus will stimulate legume production, if they are present (Jones et al. 1970; Jones and Martin 1964; Jones et al. 1983). Fertilization in the fall is particularly effective in increasing NPP (Jones 1974). Plant production from the previous year can also impact NPP. In sites with greater than 400 millimeters of rainfall per year, maximum production is associated with intermediate residual dry matter (RDM) levels of 840 kilograms per hectare. Too much RDM can suppress production the following year through shading, and too little can decrease production, presumably due to the loss of RDM's roles in microclimate mitigation, nutrient provision, and water infiltration (Bartolome et al. 2007).

Seed production from the previous year, and seedling dynamics also have strong impacts on NPP. Annual plants in California translocate 63–77% of their aboveground nitrogen to seeds (Woodmansee and Duncan 1980), over 90% of these seeds germinate at the start of the growing season, and up to 50% of germinated seedlings can die within the first six to eight weeks of the growing season. After this initial pulse of thinning, seedling death proceeds steadily throughout the growing season, so that 75–90% of seedlings die throughout the growing season (Bartolome 1979, Young et al. 1981). Seedling thinning results in inputs of very labile litter with low structural material, leading to rapid availability of seedling nitrogen to other plants. Self-thinning acts as a perfectly timed slow-release fertilizer, with release of highly labile nutrients at the time of peak plant competition (Eviner and Firestone 2007). Manipulations of seed density show that seedling thinning can double the NPP compared to planting at seed densities that are too low for thinning to occur (Eviner et al. in prep.). Similarly, increased seed density enhances aboveground productivity in other grasslands (Turnbull et al. 2000, Moles and Westoby 2006).

In fact, productivity is often so enhanced in high-density stands, that fertilizer additions cause little if any increase in productivity (while fertilizer does increase growth at low density) (Bolland 1995, Thompson and Stout 1996, Eviner et al. in prep.). Seedling thinning likely plays a role in regulating the annual variability in NPP, since these grasslands experience dramatic variations in seed production (four- to one-hundred-fold variation), seedling numbers (two- to sixfold variation), and self-thinning (one- to fivefold variation) from year to year at a given site and across sites within a given year (Heady 1958, Bartolome 1979, Young et al. 1981). Through effects on seed production, weather patterns in a given growing season may impact productivity of the following growing season. For example, winter droughts and low spring precipitation can greatly decrease seed production (Heady et al. 1992), which may lead to lower production the following growing season.

Decomposition

Breakdown of litter is critical for nutrient recycling, and for regulating excess thatch accumulation. In California grasslands, root litter typically decomposes within a year, while aboveground litter takes two to two and a half years to turn over (Savelle 1977). There are a number of key controllers of decomposition rates in grasslands. Plant senescence creates litter in the late spring, when moisture conditions are not conducive to microbial activity. Despite this, grassland litter

tends to lose 8–10% of its mass and 20% of its lignin during the first summer, due to PHOTODEGRADATION. After one year, litter exposed to sunlight in the summer has double the mass loss compared with litter that is shaded (Henry et al. 2008). As litter layers thicken, due to increased production, photodegradation effects on mass loss remain constant, but lignin breakdown decreases substantially (Henry et al. 2008). This photodegradation can have significant impacts on ecosystem carbon dynamics in the early fall. The first significant rains usually induce a 5% litter mass loss through leaching (Savelle 1977) and a respiration pulse that can be responsible for up to 10% of ecosystem carbon loss a year. These losses likely depend on photodegradation (Ma et al. 2012).

Once the rainy season begins, soil temperature and moisture determine microbial activity and decomposition rates. The peak timing of microbial decomposition roughly coincides with that of plant growth but is a bit more buffered from low temperatures (Savelle 1977, Heady et al. 1992, Eviner and Firestone 2007). Microbial activity can also persist under lower moisture conditions than plants, because they can exploit moist microsites within the soil. Because of their short generation times, microbes can respond more readily to late-season rains than plants, leading to pulses of decomposition after these rains (Chou et al. 2008). Drought conditions can decrease decomposition through moisture limitation but also through shifts in the microbial community that persist even when moisture conditions become ideal (Allison et al. 2013).

Litter chemistry is an important determinant of the rate of mass loss and nutrient release. As in other systems, higher nitrogen content of litter leads to faster decomposition rates. An important exception to this is some of the litter from forbs, which can contain defensive compounds, such as alkaloids that can inhibit decomposition (Eviner 2001). Litter structure is another key controller of decomposition rates. Standing litter that is not in contact with the soil surface decomposes more slowly than litter in contact with the surface, while buried litter is the most quickly decomposed (Dukes and Field 2000). The more litter buildup there is, the less contact there is with the soil, leading to greater inhibition of decomposition and faster buildup of litter. However, wind and rain, as well as trampling by herbivores can drive standing litter down, enhancing decomposition. Decomposition can be accelerated when litter is incorporated into the soil through gopher activity, which can decrease standing litter by two- to eightfold (Stromberg and Griffin 1996). Macrofauna, which break up litter and incorporate it into the soil, can cause 20% mass loss (Savelle 1977, Heady et al. 1992).

Nitrogen Cycling

Nitrogen is the most commonly limiting nutrient to plant growth in California's grasslands, so its cycling can be a critical controller of NPP, as well as vegetation composition (Corbin et al. 2007a, Harpole et al. 2007). Soil organic nitrogen represents 94% of the system's nitrogen pool (Eviner and Firestone 2007), but much of this is not readily available to plants and microbes, due to physical and chemical protection. Nitrogen becomes available to plants through litter decomposition, soil organic matter mineralization, atmospheric deposition, and nitrogen fixation by legumes (Woodmansee and Duncan 1980, Pendelton et al. 1983, Vaughn et al. 1986, Center et al. 1989, Heady et al. 1992). Additionally, 37% to 63% of annual internal nitrogen cycling is mediated through seed-

ling thinning, essentially acting as a slow-release fertilizer, providing nitrogen at peak times of plant nitrogen demand (Eviner and Firestone 2007). This is a key example of a driver of ecosystem processes that is unique to annual grasslands.

Like other processes, nitrogen cycling, uptake, and loss have strong seasonal trends. At plant senescence, approximately 70% of aboveground nitrogen is stored as seeds, with the remaining as litter. A range of 1% to 75% of seeds may be consumed by granivores during the summer (Heady et al. 1992), leading to potentially high nitrogen release through granivory. Summer dynamics of aboveground litter nitrogen are variable, with some studies showing loss of 25% of aboveground litter nitrogen (and 35% of root litter nitrogen) (Jackson et al. 1988), while others show nitrogen accumulation during the summer, even as mass loss occurs through photodegradation (Henry et al. 2008). This accumulation is due to microbial immobilization of nitrogen, leading to a buildup in soil microbial biomass through the summer, with its annual peak at the end of the summer (Jackson et al. 1988). Rates of nitrogen cycling can be low after spring dry-down and before the first fall rains (Herman et al. 2003, Eviner et al. 2006), but surprisingly, microbial populations and enzyme activity can be maintained through the summer (Treseder et al. 2010, Parker and Schimel 2011), leading to sustained cycling of nitrogen and accumulation of inorganic nitrogen in the soil (Parker and Schimel 2011). Part of the reason for high inorganic nitrogen accumulation is lack of moisture to facilitate gaseous and leaching losses (Eviner and Firestone 2007) as well as generally low plant uptake during the summer, because most annual plants are senesced. However, in grasslands with high biomass of summer annuals, summer uptake can be up to 10 kg N/ha, approximately 8% of the total taken up between October and June, the typical growing season (Chiariello 1989).

Fall rains stimulate nitrogen mineralization rates but have an even greater stimulatory effect on microbial immobilization and microbial biomass (Herman et al. 2003). Repeated wet-dry cycles, which are typical between fall rains, further stimulate nitrogen mineralization, microbial biomass, and microbial activity (Xiang et al. 2008). High immobilization does not prevent some nitrogen leaching loss, which is often at its peak within a few weeks after wet up (Figure 23.10) (Jones et al. 1977, Vaughn et al. 1986, Jackson et al. 1988, Davidson et al. 1990, Maron and Jeffries 2001, Lewis et al. 2006). In the winter, low temperatures cause nitrogen cycling rates to decrease, with immobilization decreasing to a greater extent than mineralization, leading to net mineralization occurring in the winter (as opposed to net immobilization in the fall) (Jones and Woodmansee 1979, Schimel et al. 1989, Davidson et al. 1990, Maron and Jeffries 2001, Herman et al. 2003, Eviner et al. 2006). Low temperatures limit plant uptake as well, leading to an increase in soil inorganic nitrogen levels (Vaughn et al. 1986, Jackson et al. 1988). Warming in early spring increases nitrogen cycling rates as well as plant and microbial uptake of nitrogen, and 82% of plant nitrogen uptake is completed by this time, even though only 45% of plant production has occurred. As the soil dries out in the spring, nitrogen cycling rates decrease (Eviner and Firestone 2007), and plant nitrogen availability may be restricted by lack of soil moisture (Everard et al. 2010). While the general seasonal trends are presented above, these seasonal patterns can vary year to year (Herman et al. 2003).

Nitrogen cycling rates also vary depending on which plant species are dominant (Eviner et al. 2006, Eviner and Fire-

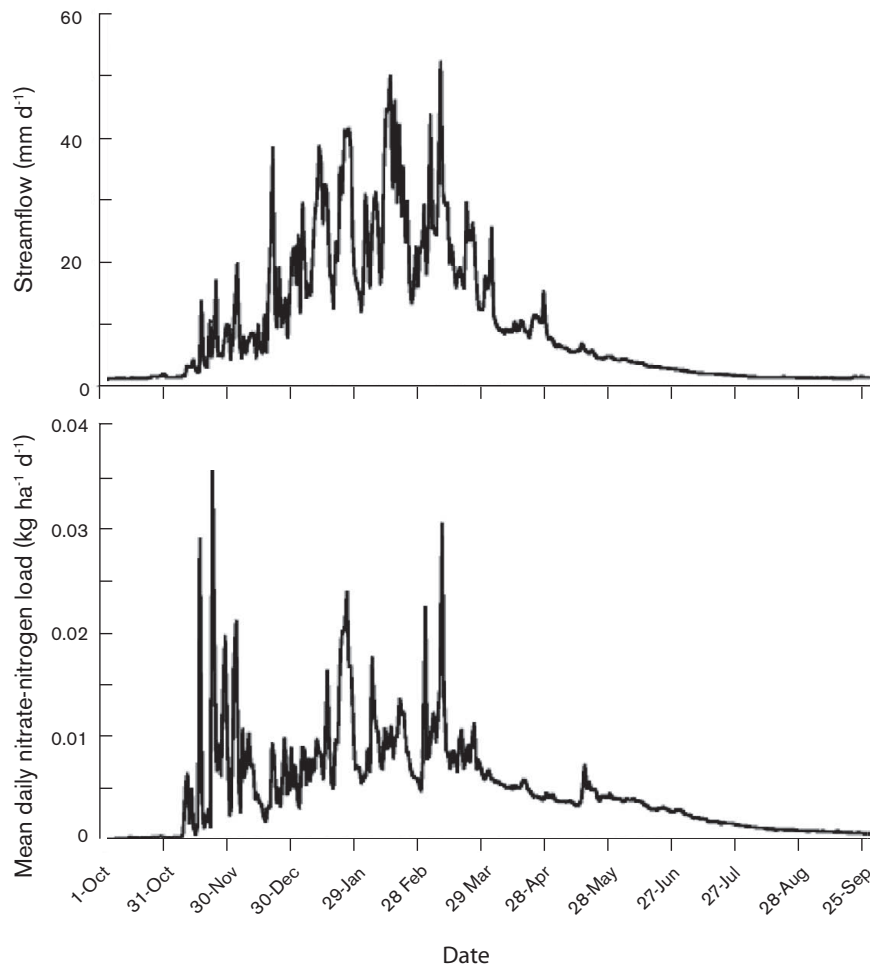


FIGURE 23.10 Seasonal fluxes of streamflow (upper) and stream nitrogen load (lower) at Sierra Foothills Research and Extension Center, by water year (October–September) from 1981 to 2000. Source: Lewis et al. 2006.

tone 2007, Corbin and D'Antonio 2011). Soil disturbance by gophers and feral pigs have the potential to increase nitrogen availability over the short term (Canals et al. 2003, Eviner and Chapin 2005), but this is not always the case (Cushman et al. 2004, Tierney and Cushman 2006, Eviner and Firestone 2007). Grazing can vary in its effects on nutrient availability, but a number of studies have indicated that grazing California's grasslands can increase soil nitrogen and sulfur but lower phosphorus (Jackson et al. 2007).

Water Balance

Water availability is the key driver of this system's structure and function, so that water inputs, infiltration, storage, and losses determine water supply for plants, animals, and humans (Parton and Jackson 1989, Reeve Morghan et al. 2007, Salve and Torn 2011, Salve et al. 2011). While water availability partly depends on precipitation inputs, the ability of the system to capture and store water is critical to support annual peak evapotranspiration in the spring, when precipitation is low and infrequent (Ryu et al. 2008). Water capture is determined by infiltration into the soil versus runoff over the surface. Early in the season, when soils are dry, water infiltration is largely determined by soil type and porosity

(determined by soil texture, soil channels from roots and soil fauna, and soil disturbance from organisms such as gophers). Standing vegetation and litter can decrease physical compaction of the soil by decreasing the impact of raindrops, and vegetation and litter also slow runoff, allowing more time for water to infiltrate into the soil. Early season rains wet up the soil surface, and with increasing rain, the soil gradually wets up deeper, creating a "wetting front." The depth and speed of this wetting front depend on the magnitude and frequency of early season rains, as well as soil channels from roots and macrofauna (Salve and Torn 2011). When small precipitation events occur, with a week or more between them, the initial soil moisture at the surface is lost due to evapotranspiration, and the next rains recharge surface soil, rather than increase the depth of the wetting front. In order to recharge soil moisture below a 0.2 meter depth, substantial rainfall over successive days is needed (e.g., 66 millimeters or more), and deep soil (1.5 meter depth) is not saturated until later in the growing season, when successive storms have occurred (Salve and Tokunaga 2000). In low rainfall years, deep soil may not be recharged (Reeve Morghan et al. 2007).

Once the soil is recharged, water storage is determined by water-holding capacity of the soil, which is determined by soil texture, organic matter, and depth. Precipitation beyond this water-holding capacity leads to a mix of surface runoff

(due to lack of infiltration) and leaching through the soil column and into the groundwater and/or streams. Because much of the rain falls at a time of low plant growth and evapotranspiration, 19–76% of precipitation can be lost through streamflow (Nixon and Lawless 1960, Parton and Jackson 1989, Lewis et al. 2006, Reeve Morghan et al. 2007). Initial rains tend to have lower loss to streamflow, since they are still wetting up the soil column. Once the soil column has wet up (estimated at 15 to 25 centimeters of accumulated rainfall), 70% of additional rainfall is lost to the system (Dahlgren et al. 2001, Lewis et al. 2006). Most of this is lost in limited pulses throughout the growing season (see Figure 23.10). For example, in one study, moisture moved below the top 0.5 meter of soil only during five significant rain periods, amounting to the twenty-one days of the growing season that received 71% of that year's precipitation (Salve and Tokunaga 2000). This can lead to highly variable streamflow from grasslands.

Annual evapotranspiration rates are less variable than streamflow, because most evapotranspiration occurs in the spring, when precipitation is low or has stopped for the season, and thus much of the annual evapotranspiration is derived from water stored in the soil (Ryu et al. 2008, Salve et al. 2011). Plant traits can influence the timing and amount of evapotranspiration, due to their different phenologies and rooting depths. Those with deeper roots can access soil water that is unavailable to many other grassland species and tend to be active later into the dry season (Enloe et al. 2004, Reeve Morghan et al. 2007).

Management practices can impact water dynamics. For example, in a study of long-term (thirty to forty years) grazing treatments, compared to ungrazed sites, heavy grazing increased soil compaction and bulk density, decreasing infiltration. This led to heavily grazed plots having two- to five-fold higher runoff and a twofold reduction in water storage. The effects of light grazing were more similar to ungrazed than heavily grazed treatments (Liacos 1962). Conversion of woody systems (oak woodlands, chaparral, coastal sage scrub) to grasslands also has large impacts on water dynamics, increasing streamflow by an average of 60%, due to lower evapotranspiration rates. However, grasslands have higher infiltration rates than woody systems, leading to more gradual release of water into streams. This results in lower maximum volume of peak storm streamflow (e.g., can minimize flooding) but longer periods of stormflow (Lewis 1968, Dahlgren et al. 2001). However, there are exceptions to these patterns, with removal of woody vegetation on some sites increasing deep water storage but not affecting runoff (Veihmeyer 1953).

Ecology and Management of Ecosystem Services

California grasslands have the potential to provide a number of key ecosystem services, including forage and livestock production, weed control, pollination, carbon sequestration, water supply and purification (including erosion control), fire control, recreation, and scenic vistas (FRAP 2010, Cheatum et al. 2011, Ferranto et al. 2011). In addition, maintenance and enhancement of plant and wildlife diversity is a key management goal in many restoration and conservation efforts and is important in enhancing the delivery and resilience of most ecosystem services. This section highlights successful management strategies for ecosystem services, although it is

important to keep in mind that the effects of management are constrained by environmental factors, which can have a strong impact on any of these ecosystem services (see Figure 23.1) (Jackson and Bartolome 2007). This results in strong site-specific and year-specific effects of management, requiring adaptive management approaches (see Chapter 37, "Range Ecosystems"). Another considerable challenge is balancing management for multiple goals, since all ecosystem services are desirable but rarely achievable simultaneously.

Focal ecosystem service goals depend on who owns the land. Eighty-eight percent of California's grasslands are under private ownership (FRAP 2003, Jantz et al. 2007), with 53% designated as agricultural (for grazing), 20% as open space, 22% as residential (at very low to low density), and 5% as "other" (Jantz et al. 2007). Fortunately, many private landowners manage for services other than forage production, with 50% or more managing for each of the following services: fire control, wildlife habitat, water quality, and erosion control. In addition, approximately 40% of private landowners actively remove non-native species and 40% plant native species (Ferranto et al. 2011).

Biodiversity

Biodiversity is a key controller of ecosystem services and is a focal goal of many conservation and restoration efforts. Even in their invaded state, California grasslands are species rich, averaging greater than fifty plant species per 30 x 30 meter area (Heady et al. 1992). California grasslands also contain a number of rare and unique habitats, including vernal pools, serpentine grasslands, and riparian systems, which are hotspots of native diversity. California's grasslands are critical habitat for diverse plants and animals, including many endemic, threatened, and endangered species. These grasslands provide habitat for nearly 90% of species in the Inventory of Rare and Endangered Species in California (Skinner and Pavlik 1994), and seventy-five federally listed threatened or endangered species, including: fifty-one plants, fourteen invertebrates, and ten vertebrates (Jantz et al. 2007). Examples of key species of concern include the San Joaquin kit fox (*Vulpes macrotis mutica*), burrowing owl (*Athene cucularia*), bay checkerspot butterfly (*Euphydryas editha bayensis*), Swainson's hawk (*Buteo swainsoni*), California tiger salamander (*Ambystoma californiense*), and California quail (*Callipepla californica*) (Barry et al. 2006, Cheatum et al. 2011).

Because 88% of California grasslands are privately owned (Jantz et al. 2007), conservation and restoration of diversity largely depends on private land owners. Large ranches are critical for wildlife conservation, providing habitat and connectivity between habitats (FRAP 2010). Wildlife are a priority for many landowners, with more than 50% managing for wildlife habitat (Ferranto et al. 2011), and many employing management strategies for specific species (SRDC 2006, Barry et al. 2006). For example, moderate grazing can benefit kit foxes, which prefer grasslands with aboveground biomass less than 560 kilogram per hectare. Mixed grazing patterns benefit burrowing owls, which prefer heavily grazed areas for nesting but require areas with tall grass cover to provide habitat for voles, their preferred prey (Barry et al. 2006). The checkerspot butterfly requires the native forb, California plantain (*Plantago erecta*), which increases in prevalence under moderate to high grazing by cattle (which prefer grasses over forbs) (Weiss 1999).

The plant community is another key focus of conservation and restoration efforts, with 40% of landowners employing management practices to decrease non-native plants and increase natives (Ferranto et al. 2011). At present, large-scale, complete eradication of non-natives is not feasible. Many restoration efforts have failed to achieve long-term self-sustaining native communities due to high rates of reinvasion of non-natives (Malmstrom et al. 2009). However, some restoration sites have been successful, particularly with repeated, long-term management of non-natives through burning, mowing, and grazing (Bossard and Randall 2007). Because of this, current restoration goals focus on decreasing weeds, while maintaining or enhancing native grasses and forbs (Stromberg et al. 2007). These restoration efforts focus on three stages: reducing non-natives, restoring natives, and controlling reinvasion (Bartolome et al. 2007). Reducing non-natives is achieved as just described, with a combination of carefully timed grazing or burning, herbicide applications, thatch removal, and sometimes tillage (Bossard and Randall 2007, D'Antonio et al. 2007). Natives are then planted, either as drilled seeds or plugs (Stromberg et al. 2007). The use of local genotypes in restoration can be important, because they are best-suited for local environmental conditions (e.g., coastal versus inland, soil type), plant competitors, and management regimes (Knapp and Rice 1998, McKay et al. 2005, Bartolome et al. 2007).

Once the natives are planted, aggressive management of weeds is typical for the first two to three years (Bartolome et al. 2007). However, a number of studies have shown that the natives can be competitive with the weeds (Seabloom et al. 2003), and that annual non-natives may dominate native restoration plots for the first few years, but then natives become dominant over the long-term, even without weed management (Corbin and D'Antonio 2004, Eviner et al. 2013). While native suppression of non-natives has been documented in a few cases, this level of successful restoration is still rare and is likely limited to key environmental conditions (e.g., moist coastal sites, valley bottoms with deep soils, and access to groundwater). Most successful restoration projects require long-term, aggressive management of annual non-natives (Bartolome et al. 2007, Malmstrom et al. 2009).

Forage Production

The largest direct economic benefit of California's grasslands comes from providing forage for livestock. Grasslands annually provide 75% of California's livestock forage (Corbin et al. 2007a, CCCC 2009, Cheatum et al. 2011). Forage availability depends on aboveground plant production and the palatability of plant biomass. Palatability is strongly influenced by plant species composition, with species differing in tissue quality and in how long they remain green into the spring and summer (green forage is much more nutritious than senesced litter). High-quality forage species include legumes such as clovers and lupines, forbs such as filaree, and some grasses with longer green forage periods (e.g., Italian ryegrass) (George et al. 2001). Low-quality species include recent invaders such as yellow starthistle, medusa head, and barbed goatgrass, which have lower production and lower forage quality than the naturalized invaders and can decrease livestock productivity 50–75% (Jacobsen 1929, Pitcairn et al. 1998, Gerlach and Rice 2003, Malmstrom et al. 2009).

While environmental factors have the strongest impacts on both production and plant composition (see Figure 23.1),

short-term improvements in forage production and composition can be achieved through planting legumes and fertilizing with nitrogen, and in some areas, fertilizing with phosphorus and sulfur (Heady et al. 1992). Forage quality and production can also be increased by controlling low-quality plants (particularly invasive noxious weeds) through the use of herbicides and carefully timed grazing or burning (Heady et al. 1992, Jackson and Bartolome 2007). Grazing management is one of the most effective and flexible tools for managing vegetation composition and production (Huntsinger et al. 2007). For example, grazing to maintain threshold levels of residual dry matter (RDM) can have a positive effect on production (Jackson and Bartolome 2002). Conversely, overuse of forage in one year can reduce production in the following year. To restore forage production in degraded grasslands, ranchers have moved away from continuous, season-long grazing, and are resting pastures and employing grazing rotations during key seasons, depending on the management goal (FRAP 2003). Because of these changes in grazing management, grassland conditions have been static or improving over the past few decades (FRAP 2003).

Pollination

Many plant species in California grasslands are wind-pollinated or can self-pollinate and thus do not require pollinators (Moldenke 1976). However, this is not the case for all species, and interactions between pollinators and many forb species can be critically important for gene flow (Chiariello 1989). These grasslands support high pollinator diversity and abundance (Wood et al. 2005, Colteaux et al. 2013) and are critical for providing pollen sources for both native bees and the honey bee during seasons when surrounding crops are not flowering (Moldenke 1976). Pollination of agricultural crops relies on the proximity of wildlands (Kremen et al. 2004), and since grasslands are often adjacent to agricultural crops, grasslands support a large portion of the pollinators for California's agriculture (Chaplin-Kramer et al. 2011). The main threats to pollinators in California's grasslands are habitat loss and invasion of non-native grasses, which decrease the abundance of forbs (Black et al. 2009).

Pollinators require a diverse community of forbs, containing species that differ in phenology and morphological traits, so that collectively they bloom throughout the season and support diverse pollinator morphologies (Black et al. 2009). Diversity of forbs is particularly critical because many grassland forbs have short flowering times and vary in timing of flowering, depending on rainfall (Moldenke 1976). Restoration efforts to increase the prevalence of native forbs in California's grasslands have successfully enhanced native pollinator populations and diversity (Black et al. 2009). Forb patches should be at least 0.2 hectares but are more effective when containing a core habitat of at least 0.8 hectares, surrounded by multiple smaller patches. These forb patches should be within 150 meters to 600 meters of nesting sites and crops that need to be pollinated, given the typical flight range of bees (Black et al. 2009). Grassland management practices that are typically used to enhance forbs (grazing, burning, and mowing) can have mixed effects on pollinators. While these management practices maintain forb cover and diversity, they can also disrupt pollinators by ruining nesting sites and interfering with immediate food supply (Black et al. 2009). To the extent possible, mowing and burning should

be timed to avoid flowering, and should avoid any summer blooms, when flowers are rare (and thus more crucial to pollinators) (Black et al. 2009). For both mowing and fire, these treatments should occur on no more than 33% of the habitat per year. This is particularly critical for fire, which can cause longer-term decreases in bee populations than mowing (Black et al. 2009). Livestock can destroy nests and trample bees and consume pollinator food (particularly livestock such as sheep, which prefer forbs) (Sugden 1985). Like mowing or fire, grazing management should be timed to minimize impacts on forbs during flowering times. When this is not possible, due to the need to control for noxious grasses, grazing should occur in small areas on any given year (Black et al. 2009).

Water Quality and Supply

Almost all of California's surface water passes through grasslands and oak woodlands (Tate et al. 1999). Thus grasslands can have strong impacts on water flow and quality. As discussed with water balance, grasslands have lower evapotranspiration than woody systems, so a higher proportion of rainfall flows into streams. In addition, because grassland soils have high infiltration, they attenuate any given storm event, leading to gradual release of the storm water to the streams (Lewis 1968, Dahlgren et al. 2001). This both reduces flood risk but also allows for continued streamflow into the dry season. Since these grasslands are naturally effective in water provision and flood control, management practices should focus on not compromising water infiltration and storage. For example, minimizing high densities of livestock during the wet season can prevent soil compaction, allowing for water infiltration.

Water quality can be a key concern, since grasslands are susceptible to erosion due to typically thin soils and prevalence of steep topography (FRAP 2003). Grasslands can also be a source of nitrogen early in the growing season, when leaching rates are high (Jackson et al. 2007). However, grasslands can also serve as important filters of pathogens, nutrients, and sediments, and are effective buffer strips between agricultural and urban uplands and streams (Tate et al. 2006, Atwill et al. 2006). However, the ability of these grasslands to filter pollutants can be overwhelmed during large storms, so not surprisingly, nitrogen and sediment inputs into streams tend to be associated with high precipitation periods (Lewis et al. 2006). Grazing can be associated with impaired water quality, particularly on the North coast (FRAP 2003), but light grazing can also enhance water quality (Barry et al. 2006).

Carbon Sequestration

California's grasslands contribute significantly to regional carbon storage due to their large spatial extent, as well as high quantity of carbon storage per unit area (similar in quantity to temperate perennial grasslands, which are well known for their high carbon storage) (Silver et al. 2010). High root allocation contributes to soil organic matter storage, and rooting depth can impact the depth distribution of soil carbon. Deeper soil carbon tends to be more stable than surface carbon, as it is less likely to undergo disturbances such as gopher or earthworm activity, and decomposer activity is lower due to fewer resources (Silver et al. 2010). Across sites, soil carbon tends to increase with increasing soil clay content and is

highest in grasslands with intermediate aboveground net primary production (Silver et al. 2010).

On average, California's grasslands are carbon neutral, varying between being a weak source and a weak sink, depending on annual weather patterns (Xu and Baldocchi 2004, Ma et al. 2007, Kroeger et al. 2009). As with other ecosystem processes, carbon dynamics are more strongly affected by the seasonality of precipitation than the total annual precipitation (Ma et al. 2007, Chou et al. 2008). When late-phenology plants are present, longer growing seasons with wetter springs increase net primary production to a greater extent than decomposition (Berhe et al. 2012), resulting in net storage of soil carbon (Ma et al. 2007). However, when late-phenology plants are absent, late-season rains stimulate soil respiration but do not alter net primary production (Chou et al. 2008), leading to carbon loss. Higher rains during the winter can increase loss of soil organic matter, despite increases in net primary production, possibly due to decreased roles of iron and aluminum oxides in stabilizing soil carbon (Berhe et al. 2012).

Despite the annual source-sink fluctuations, there is potential to increase carbon sequestration in some California grassland sites, although these protocols have not been approved for carbon credits (FRAP 2010), and important trade-offs may exist. Woody species increase soil carbon storage in California's grasslands (Silver et al. 2010) but may also decrease water supply, as has happened in other semiarid regions (Mark and Dickinson 2008). It is assumed that native perennial grasses increase soil carbon storage, and observational studies have shown that soil carbon is higher under native perennials than under non-natives annuals (Koteen et al. 2011). However, in the Koteen study it is not clear whether natives preferentially establish on soils with higher soil carbon, or if they promote higher carbon in soils where they are present. Whether perennial grasses can enhance soil carbon can be more reliably determined through experimental plantings of native versus non-native plants on the same soil types, or by comparing restored versus adjacent unrestored areas that are on the same soil. Such studies have not detected a difference in total soil carbon between natives versus non-natives (Potthoff et al. 2005) but have found that the distribution of soil carbon changes. Soils associated with perennial grasses have deeper soil carbon than soils associated with annuals (Evimer et al. in prep.) and thus could lead to longer-term sequestration.

Legumes can increase soil organic matter and microbial biomass carbon (Evimer et al. 2006, Potthoff et al. 2009) but may also enhance nitrous oxide emissions, a more potent greenhouse gas than carbon dioxide. Addition of inorganic nitrogen fertilizer has mixed impacts on soil carbon, sometimes increasing soil carbon storage through increased net primary production and litter quality, but other times decreasing it through decreasing root allocation and stimulating microbial breakdown of organic matter (Conant et al. 2001). Similar to legumes, fertilizer additions have the likely trade-off of increasing nitrous oxide production. In general, grazing has mixed effects on soil carbon storage (Conant et al. 2001, Derner and Schuman 2007), and broad comparisons of grazed versus ungrazed sites in California show no consistent effects of grazing on soil carbon (Silver et al. 2010). Light grazing does not tend to impact soil organic matter in California grasslands (Jackson et al. 2007), although overgrazing that results in high erosion has the potential to greatly decrease soil carbon. Carbon sequestration will be particularly vulnerable to wildfires and droughts, so is likely to decrease in response to climate change (FRAP 2010).

Fire Control

While fires can be harmful to human infrastructure and air quality, they tend to be less of a threat in grasslands than in woodlands and shrublands (FRAP 2010). Fire control in grasslands is primarily managed through decreasing fuel load through grazing, prescribed fire, and/or mowing (FRAP 2010). The level to which thatch is removed has great impacts on fire severity. For example, a fuel load of 2,242 kilograms per hectare can lead to fires with 15-meter-long flames, while grazing to half that fuel load can limit flames to 1–3 meters long. Grazing down to 560 kilograms per hectare leaves a fuel load that cannot support a continuous fire, so only isolated patches will burn (Barry et al. 2006).

Impacts of Humans on Grasslands

As reviewed above, California's grasslands greatly changed with European settlement, largely through the introductions of non-native plants (Bossard and Randall 2007) and domesticated livestock (Allen-Diaz et al. 2007) as well as conversion of grasslands to cropping systems. Several million hectares of California's grasslands have been cultivated, with a peak of grassland conversion occurring in the late 1800s (Heady et al. 1992). More recent land use changes also strongly affect grassland structure and function. Extensive areas of grasslands were created from woody-dominated systems, particularly in the 1950s to 1960s, in an attempt to increase forage production (Standiford and Tinnin 1996). Currently in California, grasslands are the ecosystem most at risk from development (FRAP 2010). On average, over the past few decades, more than 190 square kilometers of grassland per year have been lost to vineyards, orchards, dispersed housing, and urban development, and this loss of grassland will continue in the future, particularly with losses to vineyards and urban areas (Jackson et al. 2007, FRAP 2010). Many large ranches are being subdivided, and these smaller parcels receive less management for species conservation and ecosystem services (Ferranto et al. 2011). In fact, many grassland areas are now experiencing undergrazing, where lack of fire or grazing leads to thatch buildup, domination by species such as ripgut brome, and declines in key services such as productivity, wildlife habitat, pollination, and plant diversity (Biswell 1956, Bartolome et al. 2007).

Many shifts in disturbance regimes have occurred in California's grasslands. Over the past few centuries, the hydrology of the Central and San Joaquin Valleys has been drastically altered by dams and levees, altering the types of grassland habitats supported, and preventing the flooding regimes that regularly maintained soil fertility (Corbin et al. 2007a). There have also been substantial changes in the fire regime. On the Central Coast, fires occurred every three to five years before 1880 and now occur every twenty to thirty years (Reiner 2007). In the Sierra foothills the fire return interval was twenty-five years before European settlement, then changed to seven years after settlement, and since the 1950s, fire suppression has led to rare fires (McClaran and Bartolome 1989). Particularly in areas that have reductions in both grazing and fire, these grasslands are susceptible to increased thatch buildup, higher fuel loads, and lower diversity (particularly of forbs and legumes).

Nitrogen deposition is increasingly affecting California's grasslands, but its effects are patchily distributed. Approximately 30% of California grasslands have at least 5 kg N/ha/yr deposition, with levels up to 45 kg/ha/yr in southern Cali-

fornia and 16 kg/ha/yr in northern California (Weiss 2006, Dukes and Shaw 2007). This nitrogen deposition can increase production (Dukes et al. 2005), decrease diversity (especially of forbs), and stimulate decomposition rates (Allison et al. 2013). Nitrogen additions tend to increase non-native grasses (Dukes and Shaw 2007), and nitrogen deposition rates are high enough to enhance non-native grasses on 44% of California's grassland area (Fenn et al. 2010).

Climate change is likely to have significant impacts on the structure and function of California's grasslands. In this century, temperature rises are expected of 1.7°C to 3°C under low emissions, and 3.8°C to 5.8°C under high emission scenarios (Dukes and Shaw 2007, Cayan et al. 2008), with more warming inland than on the coast (Pierce et al. 2013). Summer temperatures will become markedly hotter. A modestly cool July in 2060 will be the same temperature as our hottest July temperatures to date. Mean temperatures in the winter will also increase, but the coolest days will be as cool or cooler than they are now (Pierce et al. 2013). Warming in the winter is expected to increase production and accelerate flowering and senescence of many species (Dukes and Shaw 2007), but cooler days may make plants more susceptible to frost kill. Annual changes in precipitation are likely to be modest, but there will be marked trends in seasonal patterns (Figure 23.11). For example, in northern California, winters will be 1–10% wetter, but times of peak plant growth will be drier, with spring precipitation decreasing by 11–18% and fall precipitation decreasing 3–8% (Pierce et al. 2013). Southern California is also likely to have drier springs and falls, but unlike northern California, its winters will also be drier (1–5%) and its summers will be wetter (46–59%) due to monsoons (Pierce et al. 2013). While projections of precipitation changes are mixed (Dukes and Shaw 2007), all precipitation projections agree that there will be increased variability in precipitation across years, with increased frequency of El Niño events and a projected 1.5–2.5-fold increase in drought frequency (Reever Morghan et al. 2007, Dukes and Shaw 2007). In addition, extreme rain events are likely to increase in frequency and magnitude, with a 10–50% increase in large three-day rain events by 2060 (Pierce et al. 2013).

The effects of these changes on precipitation will depend on when the precipitation falls. Increased precipitation during the rainy season will have little impact on overall production and species composition but can increase shoot production and decrease root production (Zavaleta et al. 2003, Dukes et al. 2005). Late-season rains have variable effects, depending on the study, but responses include increased perennials (Suttle et al. 2007), increased non-natives (Suttle and Thomsen 2007), increased abundance and diversity of forbs, and increased diversity of grasses (Zavaleta et al. 2003). Warmer and drier conditions are expected to increase shrubland area at the expense of grasslands, resulting in a 14–58% decrease in forage production by the late 2000s (CCCC 2009). However, other climate scenarios predict an increase in the extent of grasslands at the expense of woody vegetation, as increased temperatures and increased frequency of droughts significantly enhance the frequency, intensity, and extent of fires, which woody species cannot tolerate (Dukes and Shaw 2007).

Elevated carbon dioxide is another change that California's grasslands are experiencing, which can lead to shifts in plant and microbial communities, independent of the changes in temperature that they can induce. The impacts of elevated CO₂ will partially offset decreases in precipitation, since elevated CO₂ increases water use efficiency of most plants, which

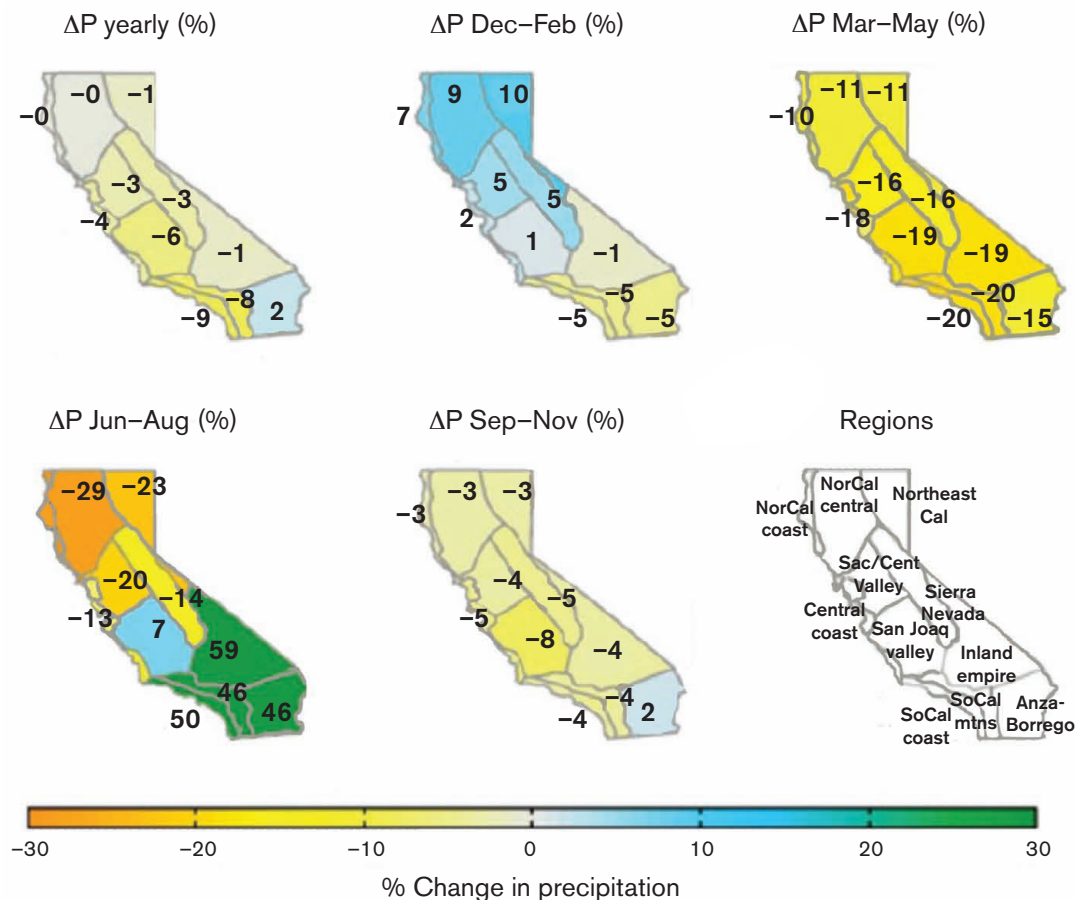


FIGURE 23.11 Predicted percentage change in precipitation (ΔP) during the period 2060–2069, compared with the period 1985–1994. Precipitation changes vary by region and by month. *Top left*: annual percentage change in precipitation. *Top center*: percentage change in precipitation over December, January, and February. *Top right*: percentage change in precipitation over March, April, and May. *Bottom left*: percentage change in precipitation over June, July, and August. *Bottom center*: percentage change in precipitation over September, October, and November. *Bottom right*: regional splits, as designated on all maps. Source: Modified from Pierce et al. 2013.

then increases spring soil moisture. This prolongs the growing season (Harpole et al. 2007) and accelerates nitrogen cycling (Dukes and Shaw 2007).

Management under Future Conditions

Managing California's grasslands under multiple environmental changes will be challenging, particularly when considering the need to balance management for multiple organisms and ecosystem services. Despite the complexity of the controls and responses of these grasslands, there are some clear challenges that lay ahead, and some relatively simple principles to consider for managing these challenges. While presented as discrete challenges, grassland managers will need integrated approaches to address all of these, simultaneously.

Management Challenge 1: The Interaction of Changing Precipitation Patterns and Non-Native versus Native Plants

While predictions of future precipitation patterns are uncertain, all climate predictions emphasize that the annual varia-

tion of precipitation will be high. There will be an increased frequency in years with shorter and drier growing seasons as well as more frequent years with longer and wetter growing seasons (CCCC 2009). Vegetation composition will vary strongly along with precipitation. Late-season rainfall benefits the most recent grassland invaders, which are noxious weeds (e.g., goatgrass, medusa head, yellow starthistle). These are a management priority for both conservation and rangeland managers because these weeds decrease plant diversity, production, and forage quality (Pitcairn et al. 1998, Gerlach and Rice 2003, Malmstrom et al. 2009). These late-season noxious weeds decline during shorter, drier growing seasons, particularly when competing with other species that can use soil moisture early in the season (Eviner et al. in prep.). Fluctuating precipitation may allow for noxious weed control through restoration of native perennial grasses. Many native grasses overlap in phenology with the late-season noxious weeds, and once established, natives can suppress these weeds by up to 90% (Eviner et al. 2013). These natives are resilient to short-term droughts but also benefit from late-season rains (Reever Morghan et al. 2007), so are likely to establish and persist under these fluctuating conditions, providing control of the late-season noxious weeds during the years that receive late rainfall.

Management Challenge 2: Managing Fragmented Grasslands for Diversity

Much of our current grassland area is under ranching, but many ranchers are uncertain if they, or future generations, will continue ranching, putting grasslands at risk for subdivision and development (Ferranto et al. 2011, Cheatum et al. 2011). As working ranches convert to dispersed housing with large properties, much less management for ecosystem services occurs, and grazing is often absent (Ferranto et al. 2011). Without grazing, thatch can build up to high levels, which can become a fire hazard, lower abundance and diversity of forbs and grasses, and decrease habitat for animals that are conservation targets, such as ground nesting birds (Barry et al. 2006). In addition, high thatch (5,000 kilograms per hectare) can increase the prevalence of noxious non-native weeds such as goatgrass and medusa head (Bartolome et al. 2007). The consequences of removal of grazers, without substituting controlled burns or mowing, has already been well acknowledged in many grassland reserves and parks, which are increasingly using short-term livestock rotations to remove fire fuel, manage non-native species, enhance plant diversity, and improve wildlife habitat (Weiss 1999, CCWD 2005, SRDC 2006). Conservation professionals will need to work with owners of small grassland parcels to implement some type of thatch removal, through controlled burns, grazing, or mowing.

Management Challenge 3: Managing for Grassland Resilience in the Face of Multiple Environmental Changes

Since California grasslands are experiencing many types of environmental changes, it is critical to consider the simultaneous impacts of these multiple changes, which can interact in important and unexpected ways (Dukes and Shaw 2007). Predicting and managing the impacts of these multiple environmental changes is challenging, particularly considering the strong spatial and temporal variation in these environmental conditions (Bartolome et al. 2007, Hobbs et al. 2007). Long-term studies have demonstrated that California's grasslands are RESILIENT to fluctuating environmental conditions due to high plant diversity. Different plant species respond to unique suites of environmental conditions, so that rare species under some conditions become common in other conditions (Hobbs et al. 2007).

Clearly, functional diversity of species is critical, but under changing conditions, there may be a loss of species with certain strategies. For example, nitrogen deposition tends to favor species with higher aboveground biomass allocation, which may lead to loss of species with higher root allocation that can withstand low soil moisture (Tilman and Downing 1994, Suding et al. 2005, Pan et al. 2011). Areas that lose these deep-rooted plants will lose a key strategy for drought resilience. To deal with these types of functional losses, managers should focus on maintaining biodiversity, while policy makers need to prioritize reversing certain environmental changes. For example, control over precipitation is much harder to achieve than reductions in nitrogen deposition, so while continued efforts should be made to mitigate climate change, we particularly need to push to decrease nitrogen emissions.

Summary

California's grasslands are distributed across a wide precipitation gradient, ranging from 12 to 200 centimeters per year (Bartolome et al. 2007). The drier interior grasslands tend to be dominated by non-native annuals, while the wetter coastal grasslands tend to be dominated by a mix of native and non-native perennials. Unique soil conditions (e.g., poor drainage, salinity, heavy metal toxicity) also define distinctive grassland types such as vernal pools, alkali sinks, and serpentine grasslands. Even within each of these grassland types, there is considerable variation in ecosystem structure and function, due to spatial and temporal variability in seasonal and annual weather patterns, topography, soil, disturbance regimes, and interactions among large herbivores, small mammals, insects, microbes, and plant communities. The predominance of annual species likely makes California's grasslands particularly sensitive to intra-annual and interannual fluctuations in abiotic and biotic controllers.

The high variability in multiple controlling factors leads to both challenges and opportunities in land management. Successful management and policy will have to shift away from a one-size-fits-all approach and embrace the reality that different techniques and guiding principles are needed from site to site, due to variations in soil, topography, and weather. In addition, at a given site, management recommendations may vary from year to year, due to high weather fluctuations (see Chapter 37, "Range Ecosystems"). Managers and scientists will need to collaborate on adaptive management approaches to understand how multiple environmental conditions interact to impact a given goal, while exploring the synergies and trade-offs associated with suites of species and ecosystem services needed from grasslands. The dominance of annuals over large areas of grasslands will require sustained management for many different goals but also provides a relative flexibility in "resetting" the system through adaptive management approaches.

Grasslands are one of the most altered ecosystems in California (Corbin et al. 2007a, Janzen et al. 2007), with non-native plant species comprising over 90% of plant cover in most areas (Bartolome et al. 2007). Despite this, California's grasslands are a diversity hotspot, averaging greater than fifty plant species per 30 x 30 meter area (Heady et al. 1992) and providing habitat for nearly 90% of state-listed rare and endangered species (Skinner and Pavlik 1994), and seventy-five federally listed plants and animals (Jantz et al. 2007). They also provide 75% of the state's livestock forage, the main direct economic benefit from these systems (Corbin et al. 2007a, CCCC 2009, Cheatum et al. 2011). These grasslands are critical in regulating water flow (e.g., flood prevention, maintaining streamflow into the dry seasons) (Lewis 1968, Dahlgren et al. 2001) and water quality (Tate et al. 2006, Atwill et al. 2006), and contribute significantly to regional soil carbon storage (Silver et al. 2010). Grasslands also support a large portion of the pollinators needed in California's cropping systems (Chaplin-Kramer et al. 2011). Because 88% of California grasslands are privately owned (Jantz et al. 2007), conservation and restoration of these grasslands largely depends on private land owners and how they balance management for livestock production, biotic diversity, and ecosystem services (SRDC 2006, Barry et al. 2006, FRAP 2010, Ferranto et al. 2011). Currently, many ranchers actively manage to improve wildlife habitat, decrease noxious weeds, and enhance water quality (Ferranto et al. 2011).

However, as working ranches convert to dispersed housing with large properties, management for ecosystem services declines (Ferranto et al. 2011), and the lack of grazing can increase fires and lower diversity of forbs and grasses (Barry et al. 2006). Other threats to grasslands include conversion to agriculture (particularly vineyards and orchards) and urban areas, and high nitrogen deposition. Climate change is likely to increase the variability in precipitation, making it more challenging to reliably manage for suites of ecosystem services. High species diversity is critical for maintaining resilience of these grasslands to changes in the means and variability of biotic and abiotic controlling factors. Rare species under one set of conditions become the dominants under other conditions, so that the species that maintain ecosystem production vary greatly across time and space in this annual grassland (Hobbs et al. 2007).

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Glossary

- BULK DENSITY** The dry mass of soil divided by its volume, used as an indicator of soil compaction.
- FECUNDITY** Reproductive capacity or output.
- FORB** A flowering plant that is herbaceous but not a graminoid (grass, sedge, rush). When the term is used in contrast with grasses, this group often includes both legume and nonlegume plants. When the term is used in contrast with grasses and legumes, it is used to denote the herbaceous species that are neither graminoids nor legumes.
- INFILTRATION** The entry of water into the soil.
- PHENOLOGY** The timing of periodic events in the life cycles of organisms, often related to climate patterns (such as seasonality). In California's grasslands the timing of plant

death in the dry spring is often categorized as early-, mid-, or late-season phenology.

PHOTODEGRADATION The degradation of molecules by the absorption of light.

RESILIENCE The ability of an ecosystem to recover from a disturbance.

SENESCENCE Programmed breakdown and death of plant tissues. In annual species this allows plants to resorb nutrients from leaves that will die and allocate those nutrients to seeds.

SOIL ORDERS The broadest classification of soils, on a global level.

SOIL SHEAR STRENGTH The ability of soil to remain intact despite force applied against it.

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