

RESOURCES

Water Relations

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California's Mediterranean-type climate has very discrete wet and dry seasons that control the availability and use of soil moisture by plants. For the graminoid species that dominate the state's grassland ecosystems, as well as most other constituents of the community, the strong seasonality of precipitation and water availability is the dominant force influencing their phenological patterns and annual productivity (Chiariello 1989). In this system, the timing of rainfall and of temperatures favorable for growth for vegetation are out of phase. As Major (1988) succinctly described:

[The state's climate] combines the very worst features of arid and humid climates. It is extremely hot and arid in summer, and extremely cool and humid in winter. The supply of water and the need for it are exactly out of phase. The productivity of natural, zonal vegetation of course reflects these climatic disabilities. The growing season is limited by the cool temperatures of winter as well as the summer drought.

In this way, California's grasslands are distinct from grasslands in North American and other temperate regions. Temporal and spatial variation in water availability play a dominant role in the species composition, productivity, and competitive interactions of California's grasslands. For example, the strong seasonality of rainfall—abundant during the winter but scarce during the summer—likely explains the strong bias in the grassland flora toward annual species (Seabloom et al. 2006). Additionally, differences in water availability between coastal and inland grasslands likely contribute to the relative importance of perennial species in coastal habitats (Elliott and Wehausen 1974; Corbin et al., Chapter 13).

In this chapter, we discuss the ecological factors that influence the availability of water to California grassland plants, including abiotic and biotic influences. Specifically, we describe the extent to which soil water availability varies

temporally, spatially, and as the species traits of the vegetation community change. We then discuss the influence of climatic conditions, including precipitation, on the productivity and species composition of grasslands. Finally, we discuss how the shift in community composition due to invasion of non-native species, including *Centaurea solstitialis* (yellow starthistle) into inland grasslands (D'Antonio et al., Chapter 6) has influenced soil moisture dynamics in California.

Patterns of Water Availability in California's Mediterranean Climate

Water availability in California grasslands varies as a result of temporal and spatial differences in moisture inputs and evapotranspiration, soil physical factors, and characteristics of plant traits that influence water uptake.

Temporal Variation

The most obvious climatic variable influencing the patterns of moisture availability in California grasslands is the strong seasonality in the period of rainfall. The existence of a subtropical zone of high pressure off Oregon in the Pacific Ocean in the summer prevents outbreaks of cold marine air from polar regions from reaching the state, resulting in a summer drought. The zone of high pressure moves further south during the winter, permitting storms to reach California and ending the drought. The net result is a strongly Mediterranean-type climate in most of the state, characterized by cool, wet winters and hot, dry summers. The period of moisture input is mostly concentrated between October and April, when, in most years, over 95% of precipitation occurs.

Even within the winter rainy season, extended periods without precipitation are regular features of California's climate. Null (2006) documented that every year between 1950 and 2006 experienced a period of at least eight days

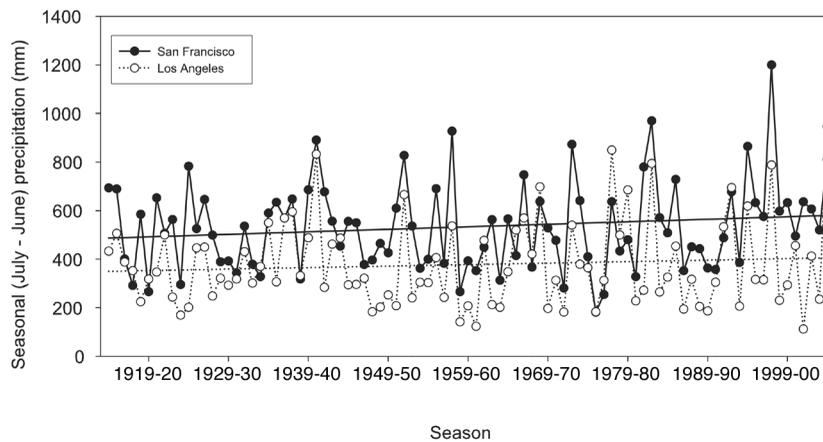


FIGURE 7.1. Seasonal (July-June) precipitation in San Francisco and Los Angeles from 1914 through 2005. Lines indicate trend lines for each location.

without rain during the otherwise wet months of December and January. The mean drought duration was 19 days; the longest was 42 days. There are indications that these “mid-winter droughts” may influence community composition in grasslands by favoring perennial grasses or forb species at the expense of annual grasses (Pitt and Heady 1978; Hamilton et al. 1999; Corbin et al., Chapter 13). For example, Hamilton et al. (1999) found that perennial grasses such as *Nassella pulchra* are less susceptible to simulated midwinter drought (35-day duration) than annual grasses. The more developed root systems of perennial grasses and forbs may make them better able to tolerate such periods of low soil water availability.

In addition to temporal variation in moisture inputs, soil moisture levels are also influenced by climatic conditions and biotic activity. The balance between water inputs and losses via evapotranspiration determine the availability of water to vegetation over the course of a growing season (Box 7.1). Here *evapotranspiration* is the sum of evaporation from surfaces, such as soil or plants, and transpiration loss through plant stomata. Potential evapotranspiration in California grasslands is highest in the warmer summer period and lowest during the winter (Major 1988). During the winter and early spring portions of the wet season there is little plant canopy area in grasslands, evaporative energy is low, and precipitation is abundant. As a result, soil moisture levels are highest. Because precipitation is generally more than adequate for plant growth during the winter, there is a soil water surplus (Major 1988). In the mid-late spring, as both temperature and day length increase, a dramatic increase in plant growth results in higher amounts of evapotranspiration and creates conditions of soil water deficit—that is, potential water loss via evapotranspiration is greater than actual water loss (Chiariello 1989). As water becomes more limited in the late spring, plant growth and evapotranspiration start to decrease; annual plants set seed and die, while perennials that cannot access deep soil water

stores or other water sources such as fog go dormant (Chiariello 1989). As the dry season progresses, plants deplete soil water stores. Summer and fall are marked by high loss of moisture via evaporative demand and no precipitation. Surface soils are typically very dry, though moisture content may be maintained at deeper soil horizons, depending on the summer activity of vegetation. Where deep-rooted vegetation can tap into deeper soil water stores, water pools over 1 meter below the soil surface may be depleted during the summer (Holmes and Rice 1996; Dyer and Rice 1999). The soil moisture that is lost over the summer via evaporation and evapotranspiration is typically recharged by the fall and winter rains. In years when wet season precipitation is low, however, there may not be full recharge of soil moisture stores. In these dry years, the surface soils may be recharged to maximum moisture content, but the deep soil layers may never reach field capacity (Box 7.1).

A water balance diagram for the growing season developed by Major (1988) suggests that California grasslands experience an annual water deficit. This water deficit may be as low as 106 millimeters in wetter areas on the northwest coast and as high as 1,089 mm in the driest sites in the California deserts (Major 1988). However, water availability to plants is limited during the hottest, driest part of the year, so total water loss through evapotranspiration is lower than it would be if California grassland soils were saturated all year.

Against the backdrop of the strong seasonality of precipitation in the state, the region also experiences significant year-to-year climatic variation (Figure 7.1). For example, although the mean seasonal precipitation in San Francisco and Los Angeles is 533 and 378 mm per year, respectively, these means do not show the tremendous range in precipitation totals. Seasonal precipitation in San Francisco has ranged over sixfold over a 22 year period, from 182 mm in 1976–1977, to 1,199 mm in 1997–1998, respectively. In Los Angeles, the range is eightfold, from 112 mm in 2001–2002

BOX 7.1 CALCULATING SEASONAL SOIL MOISTURE AVAILABILITY

In years where winter rains completely recharge soil water, we can estimate the date at which soil moisture stores begin decreasing. We can roughly determine when the net water loss begins by plotting cumulative rainfall less cumulative potential evapotranspiration for the period from February 1 through June 1. Figure 7.2 shows this type of plot for Davis in the Sacramento Valley of central California from 1995 through 1998. It illustrates the dramatic differences between years in the amount of available soil moisture and when this soil moisture becomes available. The date where the plot crosses the zero line indicates the point in time when plant transpiration begins depleting stored soil moisture, and this date is also highly variable between years. Potential evapotranspiration values, which represent the maximum soil depletion rate, can be obtained in electronic form from many weather stations that are connected to the California Irrigation Management System (Snyder and Pruitt 1992).

These calculations can be further refined by determining the potential water storage in soil. Tables in the back of USGS Soil Surveys provide estimates of the storage capacity of each soil type in a region. Storage capacity is based on soil texture and porosity. If we assume that all of the precipitation would infiltrate if given a sufficient volume of soil for its storage, the volume of the soil storage reservoir, expressed as depth in millimeters, is simply the amount of precipitation less the soil's available water storage capacity. A rough approximation of the earliest date of lethal dehydration can then be calculated by dividing the volume of the soil storage reservoir by cumulative potential evapotranspiration rate and adding the resulting number of days to the date at which evapotranspiration began to outstrip cumulative inputs (zero line in Figure 7.2).

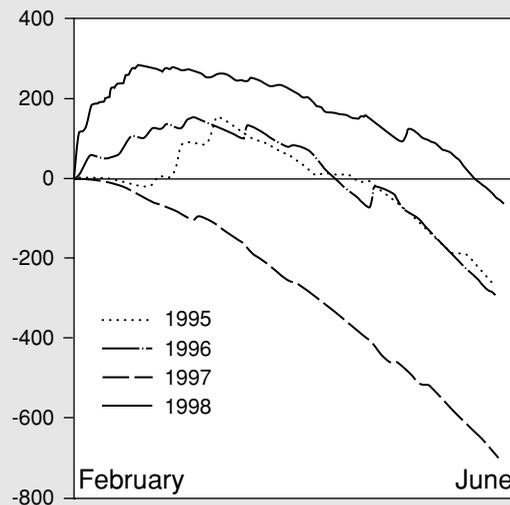


FIGURE 7.2. Cumulative rainfall minus cumulative potential evapotranspiration from February 1 to June 30 at Davis, California.

to 946 mm in 2004–2005. The years of greatest rainfall coincide with strong episodes of El Niño/Southern Oscillation (ENSO). In such years, higher than usual sea surface temperatures in the tropical waters of the central and eastern Pacific Ocean disrupt the position of the jet stream and alter worldwide precipitation patterns. The eight wettest years in San Francisco, and eight of the ten wettest years in Los Angeles, were strong or moderate ENSO seasons, as categorized by the Western Regional Climate Center (WRCC 2004). These above-average rainfall years can have a great influence on community composition and productivity in California grasslands. Global climate change could potentially increase

the frequency of ENSO events (McCarthy et al. 2001; Timmerman et al. 1999) and create dramatic shifts in composition of California's grasslands.

Years during which precipitation is well below normal, particularly when they occur in succession, can also have significant influences on the productivity and community composition of grasslands. At least eight multiyear droughts have occurred in California since 1900. Droughts that exceed three years are uncommon, though recent occurrences include 1929–1934, 1947–1950, and, most recently, 1987–1992 (Figure 7.1). Severe droughts in 1850–1851 and in 1862–1864 have been implicated in the shifts in species composition in

many grasslands from domination by native perennial bunchgrasses to domination by introduced annual grasses and forbs (Heady 1988; Major 1988; D'Antonio et al., Chapter 6). Such droughts will undoubtedly continue to influence grassland structure and function in the future, including productivity, species composition, and the range and survival of non-native introduced species.

Spatial Variation

Although the seasonal pattern of precipitation is consistent throughout much of the state, particularly within the range of grasslands, there are strong geographic differences in precipitation amounts each season. Precipitation inputs are consistently lower in southern parts of the state than in central and northern California (Figure 7.1). Mean annual precipitation also decreases as distance from the ocean increases, though not as dramatically as the north-south gradient (Major 1988). Distance from the ocean can also influence water availability, although differences in summertime conditions along a coast-inland gradient may be even more significant than differences in winter precipitation. Evaporative loss of water during the summer from interior grasslands is substantially greater than from the maritime coastal habitats, where summertime coastal fog reduces summer temperatures and evaporative energy (Major 1988). There are also differences in summertime moisture inputs between coastal and inland habitats. Coastal habitats are regularly bathed in fog during the summer (Azevedo and Morgan 1974; Ingraham and Matthews 1995; Dawson 1998), providing regular, if small, precipitation inputs that are not available to habitats outside the zone of coastal influence. This moisture input provides a substantial proportion of the water found in the tissues of perennial species in California coastal grasslands and forests during the summer drought (Ingraham and Matthews 1995; Dawson et al. 2002; Corbin et al. 2005). Finally, topography can influence precipitation; for example, the low precipitation amounts for the Carrizo Plain grasslands occur because it is located in the rain shadow of the central Coastal and Transverse Ranges.

Soil Physical Factors: Texture and Soil Depth

Soil physical factors also influence how much water a plant has access to and can use. Soil water availability to vegetation is highest when the soil is deep, plant roots have access to a large volume of soil, and soil water is held loosely, allowing free movement of moisture to plant roots (Singer and Munns 1999). In sandy soils, water is held loosely; as long as water does not drain too rapidly from these soils, it is available for easy uptake by plants (Barbour et al. 1999). Because of this loose hold on water, sandy soils tend to have lower water storage capacity than finer-textured soils. Soils with high clay content, high humus content, or both are able to store larger amounts of water, but this water is more tightly held than in sandy soils and may not be as readily taken up by plants

(Barbour et al. 1999). Research from other systems suggests that productivity in dry climates is higher in coarser-textured soils because these soils experience lower evaporative loss, while productivity in wet climates is higher in finer soils because these soils lose less water to leaching (Noy-Meir 1973). The amount of annual precipitation separating a “dry” climate from a “wet” one has been proposed as 37 cm (Sala et al. 1988) or 80 cm (Epstein et al. 1997) for the grasslands of the Central United States. Because California has a very different rainfall pattern than the Central United States does, defining it as wet or dry presents its own challenges. Soil survey data from Glenn and Tehama counties in Northern California suggest that soils that have the highest percent clay content and, thus, the highest water-holding capacity, are the most productive, but this may be a simplistic assumption (Gowans 1967; Begg 1968). More research is needed before we understand the full extent of influence that soil texture has on soil water availability in California grassland soils.

Soil depth also influences plant water uptake. Shallower soils mean less total volume of stored soil water and, therefore, less plant-accessible water. Belcher et al. (1995) observed a linear relationship between soil depth and plant above-ground biomass, reflecting the decrease in soil resources, including moisture, as soil depth decreases. Dyer and Rice (1999) found that restricted soil depth resulted in lower total soil water availability and greater water stress of *Nassella pulchra*; grasses in deeper soil produced more culms and produced those culms earlier, while grasses in shallower soil needed an extra growing season before they produced their first culms.

Plant Traits: Rooting Patterns and Phenology

Constituents of grassland communities vary in their rooting depth and architecture, so the relative dominance of different species can influence patterns of moisture availability. Rooting depth determines how much of the soil water profile a plant can access and deplete. Rooting depth, in turn, is closely related to the phenology of the various species. Species such as cool-season annual grasses, which do not survive the summer drought, do not develop roots that access deeper soil water stores. By contrast, species such as warm-season annuals and perennial species, which must maintain tissues through the summer drought, typically develop deeper root systems that can access water in deeper soil layers.

Non-native cool-season annual grasses typically concentrate their roots in the top 30 centimeters of the soil (Hull and Muller 1977; Holmes and Rice 1996). Most of these species finish their growth cycle at the end of the rainy season. This dormancy at the start of the dry season is built into annual grass physiology, and experimentally watering annual grass plots does little to delay their timing of seed formation and senescence (Jackson and Roy 1986). As a result, under annual grass-dominated sites, soil moisture availability in deeper (>60 cm) depths is relatively high (e.g., Borman et al. 1992,

Holmes and Rice 1996; Dyer and Rice 1999; Enloe et al. 2004; Gerlach 2004). For example, water relations studies on natural areas in the San Dimas Experimental Forest found that the soil moisture under an exotic spring-flowering annual grass (*Lolium multiflorum*) remained above the permanent wilting point at depths from 60 cm to 2.1 meters and was at field capacity at depths from 2.1 m to 3.6 m (Rowe and Reimann 1961; Hill and Rice 1963). However, not all cool-season annual species share the same rooting patterns as the annual grasses. For example, *Erodium botrys*, an introduced annual forb, allocated 30–35% of its root biomass to soil depths below 50 cm (Gordon and Rice 1992), and therefore could, presumably, deplete deeper soil moisture reservoirs than annual grasses could.

Warm-season forbs and grasses go through much of their growth cycle during the driest part of the year, so they require deeper rooting systems to tap into deep soil water stores. A few studies have looked at native summer-flowering annual species such as *Stephanomeria virgata* (Rowe and Reimann 1961), *Holocarpha virgata* (Green and Graham 1957), *Hemizonia congesta* (Chiariello 1989; Huenneke et al. 1990), and *Eremocarpus setigerus* (Gerlach 2004) and found that summer-flowering annuals use much more soil moisture during the summer than spring-flowering annuals. The warm-season native grasses *Aristida oligantha* and *A. ternipes* var. *hamulosa* produce root systems with both deep and shallow roots, with the deeper taproot of *A. oligantha* extending down 122 cm or deeper into the soil profile (Laude and Meldeen 1958). These plants grow throughout the summer, flower in the fall, and use deep soil moisture stores. Cutting *A. oligantha*'s taproot at 60 cm below the soil surface in late July stops access of the plant to deep soil moisture stores and results in wilting of the plant (Laude and Meldeen 1958). Rowe and Reimann (1961) reported that a native summer-flowering herbaceous dicot (*Stephanomeria virgata*) depleted soil moisture levels below 60 cm to a greater extent than the cool-season annual grass *Lolium multiflorum*.

Cool-season perennial grasses typically have a longer growing season than cool-season annual grasses, but generally do not stay active as far into the dry season as the warm-season plants do. In order to allow access to deep soil water in the first part of the dry season, they need to produce a root system that extends deeper into the soil profile than that of cool-season annual grasses. Thus, the root systems of perennial grasses are distributed throughout at least the top 60 cm of the soil profile. Hull and Muller (1977) compared the non-native annual *Avena fatua* to the native perennial *Nassella pulchra* and found that *A. fatua* roots are primarily located in the upper 30 cm of the soil profile while *N. pulchra* roots extended down to 1 m in depth. Holmes and Rice (1996) found that perennial bunchgrasses (*N. pulchra* and *Elymus glaucus*) depleted soil moisture during the summer to a greater extent than cool-season annual grasses did. The ability of perennial grasses to access such deeper stores of water during the summer, however, may be influenced by competitive interactions during the winter (Corbin et al.,

Chapter 13). Dyer and Rice (1999) found that plots containing perennial grasses and plots containing a mix of perennial and annual grasses fully depleted the soil water in shallow soil (<65 cm deep soil plots at Jepson Prairie (Solano County)). In the same study, when perennial and annual grasses were grown together in deep soil, they depleted shallow soil water stores but left water available below 60 cm. When annual-grass competition was removed, however, the perennial grasses used water much deeper in the soil profile (60–120 cm) (Dyer and Rice 1999). Thus, they concluded that competition from annual grasses can impair the ability of perennial grasses to develop deep root systems and access deep soil water stores.

Cool-season perennial grasses in the dry inland regions of California generally go dormant during the summer, with little or no green aboveground tissue and no growth. However, some of these perennial grass species have been observed to break dormancy in the fall even before the fall rains occur (Laude 1953). This means that their deep root systems remain active and able to access soil water for use in breaking dormancy and greening up. Breaking dormancy before the rainy season could allow these grasses to take advantage of the nutrient pulses released by the first fall rains.

Perennial grasses in coastal sites, may have different patterns of root distribution and activity. Corbin et al. (2005) found that coastal perennials are able to use water from summer fog as a water source and concentrate water uptake in the top 10 cm of the soil profile. Even though the soil was wetter deeper into the soil profile, the perennial grasses in their study areas maintained high shallow root biomass and active uptake near the soil surface to take advantage of regular fog deposition. Thus, these coastal grasses are less likely to deplete deep water sources as long as shallow soil water is available.

Effects of Water Availability on Vegetation Composition and Productivity

Because of the economic importance of grassland ecosystems to rangeland activities, researchers have tried to develop methods to predict productivity of grasslands from climatic conditions (e.g., Duncan and Woodmansee 1975; Pitt and Heady 1978; George et al. 1989). Pitt and Heady (1978) used stepwise multiple regression to relate weather conditions (including monthly temperature and rainfall values) and community composition in annual grasslands at Hopland Field Station, and they found broad support for the use of climate as a predictor for grassland productivity (NPP, or standing crop in annual grasslands) and community composition. Interestingly, total seasonal rainfall was not a good predictor of annual NPP. Instead, the timing of the rainfall was more important than the total amount; grassland standing crop was positively correlated with rainfall levels in the mid-winter months of December, January, and February but negatively correlated with rainfall levels in March and April.

TABLE 7.1
Variation in Average Annual Precipitation and Spring Peak Standing Crop for California Grasslands along a North-South Gradient

Location	Annual precipitation (cm)	Peak standing crop (kg/ha)
Northern sites	150–160	30–35
Central sites	65–100	20–45
Southern sites	16–20	5–15

NOTE: Data summarized from Bartolome et al. (1980).

(Abundant precipitation in the spring is associated with cool weather in the Hopland region, thereby decreasing productivity.) Climatic conditions at the time of germination also have strong influences on NPP of annual ecosystems. Pitt and Heady (1978) found that NPP was positively correlated with temperatures in October and November. Because temperatures during the December–February period are cool enough that growth rates slow considerably (Pitt and Heady 1978; Gulmon 1979), late rains or dry autumns may influence the period during which productivity approaches its highest levels.

Temperatures at Hopland influenced NPP, as well (Pitt and Heady 1978). Standing crop in March and June was positively correlated with warm mean temperatures from November through February. Standing crop in June was also negatively correlated with dry conditions in the months October, November, March, and April.

Finally, productivity is influenced by latitude. The variation in rainfall amount from north to south creates a gradient in maximum productivity, with Northern California sites tending towards higher peak standing crop than Southern California sites (Table 7.1).

The quantity of rainfall and temperatures at the time of germination affect both seedling numbers and species composition in annual grasslands (Murphy 1970; Pitt and Heady 1978). Climatic conditions early in the season have been shown to influence seedling densities, as well as the relative abundance of seedlings within the annual community. The existence of significant variation in early growing season conditions, and the responses of standing crop and species' relative abundances to these climatic conditions, have led to the widespread acceptance that the relative cover of different components can be predicted from the conditions at germination (e.g., Talbot et al. 1939; Pitt and Heady 1978). According to this "grass, clover, filaree year" framework, annual grasses are favored in years when germinating rains begin early (while temperatures are still warm) and moisture input through the autumn and winter is regular. Other community components are favored in years where germinating rains are delayed into November or December (when temperatures are colder) or when fall rainfall is sparse.

The absence of droughts during the growing season, particularly during the fall and spring, encouraged dominance by grasses; the exact importance of particular grass species varied according to other climatic conditions such as freezing temperatures during the winter. Warm and dry conditions after germination (October and November) and drought in the spring were associated with *Erodium* (filaree). Dry autumns with rainfall in the late fall or early winter encouraged clovers, though this effect was, most likely, due to decreased production of annual grasses rather than due to a positive effect on clovers.

The effects of climate change on grassland community composition and productivity are the subject of increasing attention (Dukes and Shaw, Chapter 19). A three-year study at Jasper Ridge (Santa Clara County) measured grassland responses to conditions simulating climate change, including increases in precipitation, and saw strong interactions among global change components (Shaw et al. 2002). Increases in net primary productivity due to increased precipitation as a single factor were counteracted by increases in CO₂ in multifactor manipulations (Shaw et al. 2002). Increased precipitation also changed functional group abundance (Zavaleta et al. 2003b). Changes in air CO₂ concentration, temperature, and precipitation resulted in a 50% increase in the abundance of forbs, which would greatly change the structure and function of California's grasslands. (For more detail on the interaction of increased precipitation with N deposition and climate warming as they might affect grassland soil water potential and productivity, see Dukes and Shaw, Chapter 19). In addition to the Jasper Ridge climate change study, Thomsen et al. (2006b) found that increasing the length of the growing season by artificial spring rainfall events increased grassland susceptibility to invasion by a cold-season European perennial grass. Suttle and Thomsen (Suttle et al. 2007) did not find strong effects of elevated winter rainfall on grassland productivity. Further research will help us develop a deeper understanding to predict how new changes, and their subsequent effect on water relations, will change the California grassland communities.

The Legacy of Community Conversion on Soil Moisture Patterns

California's Central Valley grasslands currently consist of a mix of annual and perennial grasses and forbs, with non-native annual grasses dominating in many areas. However, research suggests that perennial bunchgrasses were once a prominent component of many of these grasslands. It is important to note, however, that recent research suggests that not every site currently dominated by non-native annual grasses was once a perennial grassland (Hamilton 1997a; Holstein 2001). In the sites that were once perennial grasslands, the introduction of non-native annual grasses, in conjunction with drought, overgrazing, and conversion of grasslands to agriculture, resulted in loss of most stands of native perennial grasses (Burcham 1957; Dasmann 1973;

Heady 1988; Menke 1989). Because of the difference in rooting pattern and soil water access between perennial and annual grasses, the conversion of California grasslands from perennial to annual systems may have resulted in hydrological changes to grassland soils and, most importantly, an increase in deep soil moisture.

The increase in available soil moisture following grassland conversion in sites that previously were dominated by perennial grasses may have promoted the establishment and spread of new invaders (i.e., “Fluctuating Resource Theory of invasion”; Davis et al. 2000). One invader that may have taken advantage of increased soil moisture is the deep-rooted invasive forb *Centaurea solstitialis* (yellow starthistle). *C. solstitialis* is able to use deep stores of soil water, and may deplete even deeper stores of soil moisture than those used by perennial grasses. For example, Enloe et al. (2004) created communities dominated by *C. solstitialis*, annual grasses, or perennial grasses and measured soil water content at depths from 30 to 150 cm over three growing seasons. They found that soils under *C. solstitialis* contained a water content of $18.35 \pm 0.24\%$, while under annual grasses the soil water content was $22.76 \pm 0.24\%$, and under perennial grasses the soil water content was $19.74 \pm 0.28\%$. Thus, soils under *C. solstitialis* were significantly drier than soils under annual grasses, with soil moisture levels under perennial grasses intermediate between the two (Enloe et al. 2004). In a study in southwest Oregon, Borman et al. (1992) compared the depletion of soil moisture by annual grasses, perennial grasses, and *C. solstitialis*. They found that plots dominated by annual grasses had around 50% higher soil moisture than plots dominated by perennial grasses or *C. solstitialis*. Similarly, Gerlach (2004) found that perennial grasses extract more deep soil water than annual grasses do and, in some studies, have been shown to extract as much deep soil water as *C. solstitialis*.

Thus, the invasion of California’s Central Valley perennial grassland sites by annual grasses may have left deep soil moisture resources untouched and promoted the invasion of these sites by *C. solstitialis*. Simberloff and Von Holle (1999) call the process whereby early invaders facilitate invasion by later species, eventually resulting in the total loss of native species, “invasion meltdown.” Because research has shown a positive correlation between *C. solstitialis* invasion success and soil water availability during late spring and summer (Dukes 2001a), it appears that the conversion of California grasslands to native annual grass dominance and subsequent widespread starthistle codominance is a case of invasional meltdown.

We may be able to reverse the decrease the availability of deep soil moisture and reduce *C. solstitialis* invasion by restoring grasslands with native perennial grasses. Both *C. solstitialis* and *Nassella pulchra* allocate early resources to root growth (Thomsen et al. 1989; Roché et al. 1994; Holmes and Rice 1996; Gerlach et al. 1998; Dyer and Rice 1999). Studies have found decreased cover and higher water stress in *C. solstitialis* growing in shallow or dry soils (Roché et al. 1994; Sheley and Larson 1995). Thus, if restoration of grasslands with perennial grasses can deplete deep soil water stores, we may be able to reduce the invasion success of invaders such as *C. solstitialis* (Borman et al. 1992; Roché et al. 1994). Care must be taken, however, to ensure that restoration with perennial grasses is not undertaken as a blanket approach to restoring all *C. solstitialis* sites but, instead, is used when research suggests that these perennial grasses were once an important component of the vegetation in that site; some sites may require different restoration approaches to manage *C. solstitialis* and return the site to something more similar to its original plant community.

Conclusion

Soil water availability in California grasslands varies both temporally and spatially, with vegetation characteristics such as rooting depth also having an effect on soil water access and depletion. Thus, changes in rainfall amount and timing, amount of transpiration loss through vegetation, or shifts in community composition may all influence soil moisture availability and, in turn, influence the productivity and species composition of grasslands. Because the effects of different plant species can change water availability, shifts in community composition due to invasion of non-native species have the potential to change soil moisture dynamics. We suggest that replacement of perennial grasses with more shallowly-rooted annual grasses in inland areas may have created an increase in deep soil moisture stores. This then resulted in a soil that was particularly at risk from invasion by deep-rooted *Centaurea solstitialis* (yellow starthistle), resulting in additional changes to soil moisture dynamics.

Acknowledgments

We would like to thank Meredith Thomsen, Andy Dyer, and Carla D’Antonio for their helpful comments and advice on this chapter.