

Competitive Interactions

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The diversity, species composition, and relative abundances of vegetation in California's grassland ecosystems are the result of a complex interaction between historical factors, abiotic conditions including climate and soil, and biotic interactions. The rangeland literature has frequently discounted the importance of competitive interactions between plants, arguing that many rangelands are not in equilibrium to the extent that would allow competitive interactions to drive species composition (Jackson and Bartolome, Chapter 17). However, a variety of studies, particularly those documenting interactions between perennial species but also interactions between annual species, have demonstrated that competitive interactions play an important role in determining the presence and relative abundances of grassland species. In the following sections, studies that have examined competitive interactions in California grasslands are reviewed, and life history characteristics, including longevity, growth patterns, and productivity, that influence competitive outcomes are considered.

For the purposes of this review, competition is defined as the interactions between plants that result in decreased performance (measured by fitness, productivity, or survival) of one or more community constituents. Often, the competitive impacts take relative abundances of each competitor into account, rather than measuring impacts on a per individual basis. Indeed, the competitive superiority of exotic annual grasses in many grasslands is understood only when the large number of individuals per unit area is taken into account. In cases in which results from controlled experiments are examined, competitive outcomes are often measured as decreased performance in the presence of another individual or species as compared to the performance in the absence of other individuals or species. In the cases of observations of patterns in natural landscapes, including the competitive dominance of certain species (i.e., exotic annual grasses) under particular conditions, results of competition are inferred by numerical or functional superiority. Admittedly, this is an

indirect measure of competition that does not control for other important factors such as herbivory, propagule limitation, or edaphic conditions. However, numerical or functional superiority is still a useful indicator of competitive dominance in this system as long as certain caveats are recognized.

First the major components of grassland communities are presented, including descriptions of their phenology and growth strategies. The knowledge as to the competitive outcomes between each group and how they vary with resource availability or region is also reviewed. In order to understand the mechanisms by which the competitive interactions take place, a description of how various life-history characteristics affect growth and survival and the interactions between species is presented. Finally, the question of how management strategies can be used to alter competitive interactions to favor native species, including grazing regimes and seed addition, is considered.

Components of California Grasslands

The large number of species that occur in California's grassland communities can be subdivided into broad functional groups according to phenology and/or life-history characteristics. Annual grasses, perennial grasses, and annual and perennial forbs are considered separately. The outcomes of competitive interactions between these functional groups vary temporally and spatially and can be strongly influenced by environmental conditions and/or management activities.

Annual Grasses

Annual grasses are the most important component of most grassland communities in the state, particularly in inland habitats. Species such as *Avena* spp., *Bromus diandrus*, *Bromus hordeaceus*, and *Vulpia* spp. essentially dominate all low-elevation interior habitats such as those in the interior valleys and foothills lining both sides of the Great Central Valley (Heady

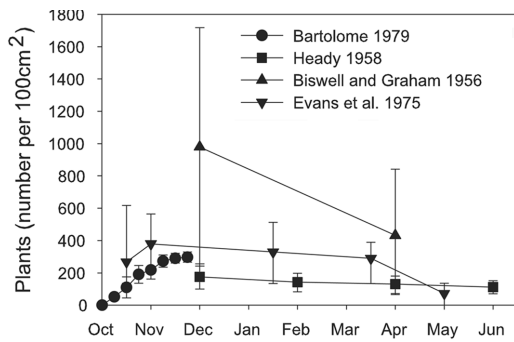


FIGURE 13.1. Density of annual plants through the growing season reported in four studies from California grasslands. Symbols represent the mean of all trials conducted in each study, while error bars represent the range (min–max) reported.

1988). These are largely species of European origin that invaded in the early eighteenth century (for further discussion see D’Antonio et al., Chapter 6). Little is known about the extent to which native annual grasses occurred in grassland habitats prior to the conversion; today native annual grasses such as *Vulpia microstachys* are much reduced in their distribution and abundance.

The majority of annual grass seeds respond quickly to the onset of the fall rains, which typically occur by mid-November. Bartolome (1979) reported near-maximum seedling densities for several species, including *Vulpia* spp., within 1–2 weeks following rains sufficient to stimulate germination (Figure 13.1). Other annual grasses, such as *Aira caryophyllea*, exhibited a more conservative strategy and germinated later. After the first 1–2 months, however, the number of germinable seeds remaining in the soil declined to very low numbers.

After establishment, annual seedlings grow rapidly as long as conditions remain favorable (Gulman 1979), but productivity slows considerably during the winter months as average temperatures drop and light availability decreases (Table 13.1) (Pitt and Heady 1978; Gulman 1979; Chiariello 1989). During the winter (December–February), when resource demand is low, density-dependent mortality is minimal (Gulmon 1979). In early spring (March–April), temperature and day-length increase and soil moisture levels are favorable for growth, which leads to a period of rapid biomass production (Table 13.1) (Savelle 1977; Pitt and Heady 1978; Gulmon 1979; Chiariello 1989). The dense stands of annual plants experience extensive self-thinning—as high as 50–75% (Eviner and Firestone, Chapter 8)—throughout the remaining vegetative period (Figure 13.1) until plants begin producing reproductive structures. Annual grasses such as *A. caryophyllea* may complete their life cycle by April 1 while others, such as *Aegilops triuncialis* or *Bromus diandrus*, may reach senescence in early June.

Perennial Grasses

California’s grasslands are assumed to have been largely dominated by perennial grasses prior to European settlement in the nineteenth century (D’Antonio et al., Chapter 6; Hamilton

1997a; Heady 1988). Today, perennial grasses are relatively rare in inland habitats, though they may dominate coastal habitats (Heady 1988; Peart 1989a; Stromberg et al. 2001). The most widespread of the native perennial grasses is *Nassella pulchra* (purple needlegrass), which can be found in both the more mesic northern coastal grasslands and the hotter, drier interior and southern grasslands. Remnant coastal prairies may be dominated by such native species as *Danthonia californica* (California oatgrass), *Festuca rubra* (red fescue), and *Deschampsia caespitosa* (tufted hairgrass). Exotic perennial grasses, including *Holcus lanatus* (velvet grass), *Festuca arundinacea* (tall fescue), *Phalaris aquatica* (harding grass), and *Dactylis glomerata* (orchard grass), dominate many other coastal habitats, particularly ones that have been disturbed and that are not grazed.

Phenology of perennial grasses is relatively similar to that of annual grasses with germination in the fall and greatest growth during the winter and early spring. However, while annual species develop from seedling to flowering adult over the course of about 6 months with relatively little variation aside from climatic influences, the length of time to maturity of perennial species can be indefinite (Dyer et al. 1996). Perennial grasses can reach the flowering stage within a single growing season or take several years, depending on a wide variety of biotic, abiotic, and edaphic factors. The most obvious difference between annual and perennial grasses is the presence of green tissue in perennial grasses later into the summer. In coastal habitats, where cooler temperatures, greater cloud cover, and the frequent input of moisture from fog moderates summertime conditions (Azevedo and Morgan 1974; Ingraham and Matthews 1995; Corbin et al. 2005), perennial species are able to maintain biological activity during the summer while most annual species die back.

Annual and Perennial Forbs

Herbaceous forb species that are widespread in California grasslands include the native species *Eschscholzia californica* (California poppy), *Calochortus* spp. (Mariposa lilies), *Hemizonia* spp. (tarweeds), and the exotic species *Erodium* spp. (filaree), *Cirsium* spp. (thistles), and *Centaurea solstitialis* (yellow starthistle). This group also includes important nitrogen fixers such as *Lupinus* spp. (lupines), *Trifolium* spp. (clovers), and *Lotus* spp. Forbs make up a significant component of grassland biodiversity (Hayes and Holl 2003a) and are responsible for the wildflower displays for which California grasslands are famous; they are also some of the most widespread and problematic weeds in the state (DiTomaso et al., Chapter 22; Cal-IPC 2006).

Competitive Interactions

In the vast majority of grassland habitats in the state, exotic annual grasses dominate communities in terms of both cover and biomass. Important exceptions include coastal prairie grasslands along the central and northern coast,

TABLE 13.1
Growth rates of total aboveground biomass at an annual and
perennial (*Nassella pulchra*)-dominated site at Hopland Field Station

Annual Site			Perennial Site	
Sampling period	Absolute g / day	Relative mg / g / day	Sampling period	Absolute g / day
1970–1971				
Oct 21–Dec 7	0.340	42.5	Oct 21–Feb 1	0.549
Dec 7–Feb 8	0.377	13.4		
Feb 8–Mar 6	1.077	19.1	Feb 1–Mar 1	0.893
Mar 6–Apr 4	2.897	23.9	Mar 1–Apr 1	2.065
Apr 4–May 5	4.806	14.9	Apr 1–May 1	3.867
May 5–June 2	0.857		May 5–June 2	4.057
1971–1972				
Nov 13–Dec 4	0.524	95.3	Nov 13–Jan 16	0.406
Dec 4–Jan 3	0.233	16.1		
Jan 3–Mar 2	0.814	14.5	Jan 16–Mar 1	1.000
Mar 2–Apr 1	3.811	21.5	Apr 15–May 28	1.163
May 8–June 5	0.939			

NOTE: (Saville (1977). Absolute growth rate is the increase in biomass per day, while specific growth rate is the increase in biomass per day per average amount of biomass present during the sample period.

where perennial grasses frequently dominate (Heady 1988; Stromberg et al. 2001). Another exception is found in seasons where annual forbs—including *Erodium* spp. and *Trifolium* spp.—approach or even exceed the cover and biomass of exotic annual grasses. For the most part, the conditions that give rise to these “forb years” are ones in which temperature or precipitation patterns during germination and early growth are unfavorable to grass growth (Pitt and Heady 1978). Annual and perennial forbs also are the dominant life-forms in edaphic habitat types such as vernal pools or serpentine grassland. It is useful to examine the specific relationships between the three groups in turn.

Annual Grasses vs. Annual and Perennial Forbs

Annual grasses dominate cover and biomass of inland grasslands in most years (Talbot et al. 1939; Heady 1958; Bartolome 1979; Heady 1988), though particular climatic conditions give rise to years in which the annual *Erodium* spp. (filaree) is dominant or when it and the nitrogen fixer *Trifolium* spp. (clover) are co-dominant (e.g., “grass-clover-filaree years”; D’Antonio et al., Chapter 6; Talbot et al. 1939; Heady 1958; Pitt and Heady 1978). In a study of botanical composition of Hopland Field Station (Mendocino County) grasslands from 1955 through 1973, Pitt and Heady (1978) found that the cover of such annual grasses as *A. barbata*, *B. mollis* (*hordeaceus*), and *Vulpia* spp. ranged from 24.1% to 82.1%. Cover of *Erodium* spp. ranged from 3.6% to 48.1%, and cover of *Trifolium* spp. ranged from 2.5% to 20.1%. At no point was *Trifolium* dominant in terms of percent cover, though it reached its highest cover in the year that annual grass cover was its lowest. Similarly, the

highest annual grass cover coincided with the lowest *Erodium* cover (Pitt and Heady 1978).

Pitt and Heady (1978) found that annual grasses were favored in years when germinating rains begin early (while temperatures were still warm) and precipitation through the autumn and winter was regular. Years in which there were late rains, or an extended winter or spring drought, favored filaree and clover, respectively. Another way of describing these patterns is to say that years with “favorable” rainfall patterns have relatively high grass cover, while years with suboptimal rainfall patterns have relatively high cover of nongrasses. Thus, annual grasses appear to be superior competitors vs. forb species as long as climatic conditions do not limit grass productivity or seedling survival.

Annual Grasses vs. Perennial Grasses

INTERIOR GRASSLANDS

A variety of experiments have demonstrated that exotic annual grasses are able to reduce the growth and survival of native perennial grass individuals and to limit the growth of native grass populations where they exist. The effect is most pronounced in the Central Valley, where competition studies between the native perennial *N. pulchra* and exotic annual grasses consistently favor the exotics (Dyer and Rice 1997b, 1999; Brown and Rice 2000; Marty 2005). The exotic annual grasses are able both to reduce the establishment of seeds and seedlings of perennial grasses and to reduce growth and survival of mature individuals. In established annual grasslands, whatever perennial seeds may be present often germinate

and emerge relatively well, but seedlings are lost rapidly as the season progresses. Rapid vertical growth by annuals quickly reduces light availability to plants of small stature (Evans and Young 1989; Dyer and Rice 1999), including *N. pulchra* seedlings. Annual vegetation does not have to be especially tall if densities are great. As the season progresses, soil water is reduced faster by annual vegetation and at higher densities (Reever Morghan et al., Chapter 7; Gordon and Rice 1992; Holmes and Rice 1996; Dyer and Rice 1999), thereby compounding the resource stress.

Annual grasses are also able to reduce growth of established *N. pulchra* individuals (Dyer and Rice 1997b; Hamilton et al. 1999). A. Dyer (2003) followed natural *N. pulchra* individuals in a Central Valley grassland dominated by annual grasses and found that 26.1% (164 of 629) of mature plants died over a seven-year period. Marty et al. (2005) reported a loss of 3–30% of adult *N. pulchra* individuals over a five-year period across a range of grazing and burning treatments at Beale Air Force Base (Yolo County). Hamilton et al. (1999) found that mature *N. pulchra* individuals at Hastings Reserve (Monterey County) were more water stressed and produced between 1.6–3.5 times fewer seeds per plant in the presence of exotic annual grasses, but there was no net loss of natural *N. pulchra* over a 25 year period. Differences in responses of *N. pulchra* populations between the Central Valley locations of A. Dyer (2003) and Marty et al. (2005) vs. the more mesic Hastings Reserve of Hamilton et al. (1999) suggests that *N. pulchra* populations growing in mesic vs. xeric grasslands may respond differently to annual competitors.

The negative effects of exotic annual grasses on all *N. pulchra* life stages—seed, seedling, and adult—strongly suggest that the exotic annuals have a negative effect on many native perennial populations. Even under the best of circumstances, native perennial grasses tend to be relatively minor components (in terms of cover or biomass) in inland grasslands (Heady 1988; Stromberg and Griffin 1996), and the long-term stability of the perennial populations—increasing, decreasing, or stable—is rarely known. Further research is needed to understand the population dynamics of native species in exotic-dominated grasslands, to identify vulnerable life stages, and to design management strategies that will ensure persistence (Box 13.1).

Whether perennial grasses are increasing or decreasing in abundance, or have been excluded altogether, depends on the seasonal timing of competitive stress relative to perennial phenology—particularly whether seedlings are able to develop root systems that are sufficient for the individual to survive the summer drought. Furthermore, grazing and burning treatments may moderate the intensity of competition between annuals and perennials and perhaps allow the perennials to coexist. Positive effects of treatments such as grazing may also work in combination with other factors. For example, Dyer and Rice (1997b) found that grazing reduced the negative effect of herbivory by gophers on *N. pulchra*. Management strategies such as grazing that may alter

competitive relationships between annual and perennial grasses are considered later in this chapter.

COASTAL GRASSLANDS

In contrast to inland grasslands, competitive interactions in grasslands along the central and northern coasts consistently favor perennial species. Corbin and D'Antonio (2004b), working in a Marin County coastal prairie, found that the presence of native perennial grasses reduced aboveground biomass of exotic annual species by as much as 80%. In contrast, while native perennial grasses, planted as seedlings, experienced a negative effect of the presence of exotic annual grasses in the first year following planting, the negative effects of the annuals decreased when the perennials were 2, 3, and 4 years old. In fact, biomass of 4-year-old native perennial grasses grown with exotic annual grasses was not significantly different from the biomass of natives grown without exotics. Similarly, Seabloom et al. (2003b) found reduced cover and fecundity of annuals in established multispecies perennial grass plots at the Sedgewick Reserve (Santa Barbara County).

The persistence of relatively undisturbed remnant coastal prairie grasslands further illustrates the competitive ability of native perennials in coastal habitats and their ability to resist invasion by exotic annuals. In Stromberg et al.'s (2001) survey of coastal prairie grasslands in central California, the exotic grasses that were most abundant—*Vulpia myuros*, *B. hordeaceus*, *A. caryophyllea*, and *Briza minor*—were relatively small-statured compared to the species, such as *Bromus diandrus* and *Avena* spp., that dominate many inland grass communities. Mean species richness (per m²) was also higher in the coastal grasslands (22.6 species) vs. inland grasslands (14.7 species), and the ratio of exotic to native species richness was lower.

In sharp contrast to their dominance in most interior and southern grasslands, annual grasses are frequently relatively minor components of the coastal grassland community or are relegated to recently disturbed patches. Peart (1989b, 1989c), studying colonization of intact and disturbed grassland patches at Sea Ranch (Mendocino County), found that annual grasses such as *V. myuros* persist in mixed annual–perennial patches mainly as colonizing species following small-scale disturbances (e.g., gopher mounds). *V. myuros* was able to colonize mounds in the first year following disturbance but was excluded by perennial species in the following year (Peart 1989c). Patches where *V. myuros* dominated were also highly susceptible to invasion by exotic perennial grasses such as *Anthoxanthum odoratum* and *Holcus lanatus*. By contrast, *V. myuros* was unable to invade and persist in undisturbed patches dominated by perennial grasses (Peart 1989b).

Climatic conditions in coastal habitats are significantly more mesic than in interior grasslands, owing to the cooler temperatures, greater cloud cover, and the frequent input of moisture from coastal fog (Azevedo and Morgan 1974;

BOX 13.1 MODELING POPULATION GROWTH OF *NASSELLA PULCHRA*

Matrix models are useful to estimate the intrinsic rate of increase (λ) of a population, or to assess particular stages that are critical to the demographics of a population (Caswell 1989). We used a simple stage-based matrix model to calculate λ of *Nassella pulchra* based on available estimates of the proportion of individuals that survive the transition from each stage to the next. We included four life stages: seeds, seedlings, reproductive adults, and a senescent, nonreproductive stage (Figure 13.2). The latter stage was included to truncate the lifespan of these potentially long-lived grasses (Hamilton 1997), in lieu of detailed data on the shape of survivorship curves. The effect of this senescent stage should be to decrease estimates of λ . We set all parameters based on published data (Tables 13.2 and 13.3). We included only situations in which native perennial grass seed was added to intact plant communities—we excluded studies in which the vegetation was disturbed or manipulated to enhance seed survival.

The model suggests that the perennial lifestyle imparts a competitive advantage. Perennial grass populations can have positive population growth rates even when seedling survival in the first year is exceptionally low. This result is robust to adult lifespan and suggests that it may be generally true for many species of perennial grasses. While we predict successful establishment in the majority of cases, there were cases in which survival through the first year was insufficient to create positive population growth rates, namely samples in the lowest quartile in Figure 13.3. In these cases, it is likely that the presence of exotic annual competitors precludes seedling establishment.

TABLE 13.2
Survival During First Year in Experimental Seed Additions in California Grasslands.

<i>Data source</i>	<i>Year</i>	<i>County</i>	<i>Sown species</i>	<i>Species type</i>	<i>Grassland type</i>	<i>Percent survival</i>
Robinson et al. 1995	1983	Yolo	<i>Eschscholzia californica</i>	Perennial forb	Exotic annual	0.14
Seabloom et al. 2003b	1998	Santa Barbara	<i>Lasthenia californica</i>	Perennial forb	Exotic annual	60.83
Seabloom et al. 2003b	1998	Santa Barbara	<i>Plantago erecta</i>	Annual forb	Exotic annual	39.82
(Brown and Bugg 2001)	1993	Yolo	Annual forb mix	Annual forb	Exotic perennial	7.20
Gillespie and Allen 2004	2001	Riverside	<i>Erodium macrophyllum</i>	Annual forb	Exotic perennial	3.00
Robinson 1971	1967	Monterey	<i>Nassella pulchra</i>	Perennial grass	Exotic annual	59.00
Brown and Rice 2000	1993	Yolo	Mix of native species	Perennial grass	Exotic annual	6.62
Robinson 1971	1966	Monterey	<i>Nassella pulchra</i>	Perennial grass	Native perennial	0.00
Robinson 1971	1967	Monterey	<i>Nassella pulchra</i>	Perennial grass	Native perennial	39.75
Dyer et al. 1996	1989	Yolo	<i>Nassella pulchra</i>	Perennial grass	Native perennial	1.10
Dyer et al. 1996	1990	Yolo	<i>Nassella pulchra</i>	Perennial grass	Native perennial	0.20
Hamilton et al. 1999	1995	Santa Barbara	<i>Nassella pulchra</i>	Perennial grass	Native perennial	15.00
Peart 1980	1980	Sonoma	Mix of native and exotic grasses	Perennial grass	Exotic perennial	0.57
Peart 1980	1980	Sonoma	Mix of native and exotic grasses	Perennial grass	Exotic annual	2.70
Peart 1980	1981	Sonoma	Mix of native and exotic grasses	Perennial grass	Exotic annual	0.18
Peart 1980	1980	Sonoma	Mix of native and exotic grasses	Perennial grass	Native perennial	1.16

NOTE: Seed was added into intact plant communities without further management. We treat seed additions in separate years or plant communities as unique replicates, although they are published in a single study. We do not analyze species-specific responses of species sown in a single mixture to control for among-seedling interactions.

BOX 13.1 (continued)

TABLE 13.3
Parameter Values Used in Perennial Grass Matrix Model

Parameter	Definition	Value	Reference
f_{31}	Fecundity of reproductive adults (seeds per plant)	26-95 ^a	Hamilton et al. 1999
p_{12}	Probability of seed becoming a 1-year seedling	0.001 to 0.3	Values from Table E1 for native perennial grasses
p_{23}	Probability of 1-year seedling becoming a reproductive adult (stage 3)	0.71-0.88 ^b	Shoulders 1994
p_{34}	Probability of a reproductive adult becoming senescent (stage 4)	$(1 - p_{33})$	Defined by p_{33}
p_{33}	Probability of a reproductive adult remaining reproductive (stage 3) into the next year	0.5 to 0.9	Shoulders 1994, Hamilton et al. 1999
p_{44}	Probability of a senescent adult remaining alive to the next year	0.1	Arbitrarily low to ensure rapid mortality

^a Hamilton measured seed production of adult *N. pulchra* plants in control plots that received 330 mm of precipitation and in watered plots that received a total of 610 mm.

^b Shoulders measured survival of transplanted *N. pulchra* plugs in a dry (280 mm) and wet (784 mm) year.

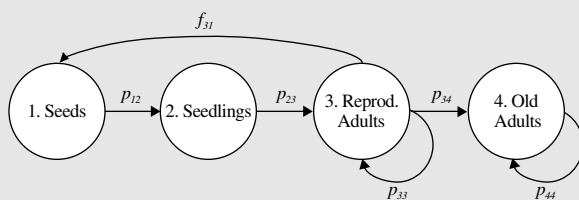


FIGURE 13.2. Schematic of matrix model used to calculate perennial grass population growth rates. The perennial grass life is represented in four stages: 1. seeds, 2. one year old seedlings, 3. reproductive adults, and senescent adults.

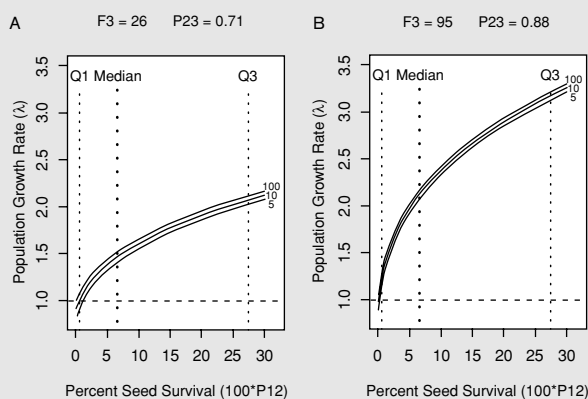


FIGURE 13.3. Effects of first year survival (p_{12}), second year survival (p_{23}), mean adult lifespan ($1/(1-p_{33})$), and adult fecundity (f_3) on predicted growth rates of perennial grass populations. Mean lifespan is labeled on graph (5, 10, and 100 years). Dashed horizontal line shows the point of no net population growth rate ($\lambda=1$). The first quartile, median, and third quartile of empirical estimates of p_{12} are shown as vertical dotted lines. The two panels illustrate predictions for two scenarios: (a) low precipitation (280–330 mm) and (b) high precipitation (670–780 mm).

It should also be noted that the seedling survival estimates used in this modeling exercise are based largely on experiments using *N. pulchra*, a species that may have very low seedling survival relative to other native perennial grasses (Seabloom, unpublished data). In addition, the model did not allow reproduction until the third year in order to mimic the slow growth of *N. pulchra*. In reality, many perennial grasses seed in their first and second year (e.g., *Bromus carinatus* and *Elymus glaucus*). Models that include seed reproduction in year two have dramatically higher population growth rates (results not shown). For these reasons, the model simulations shown here are conservative estimates of the potential population growth rates for the native perennial grass community as a whole.

Ingraham and Matthews 1995; Corbin et al. 2005). As a result, the balance between evapotranspiration and water availability is significantly more favorable than in hotter and drier regions such as those inland, and perennial species are able to maintain biological activity during the time that winter annual species die back. Perennial species, including native and non-native grasses, have been shown to take up moisture from coastal fog via shallow roots, thereby moderating the effect of the summer drought (Dawson 1998, Corbin et al. 2005). As distance from the coast increases or where topography blocks the marine influence, evapotranspiration increases and moisture inputs from coastal fog decrease. The importance of these climatic differences for the competitive relationship between annual and perennial grasses is discussed later in the chapter.

Perennial Grasses vs. Perennial Grasses

Though the invasion of coastal grasslands by exotic annual grasses is frequently less severe than in inland grasslands, another group of grasses—exotic perennial grasses—have a significantly stronger ability to invade. Greater moisture input and lower evapotranspiration during the summer (Chapter 7; Corbin et al. 2005) may favor perennial species—native and exotic—over annuals. Exotic perennial grasses such as *H. lanatus*, *Festuca arundinacea*, *Phalaris aquatica*, and *Dactylis glomerata* dominate many coastal grassland habitats, particularly ones that are not grazed (Heady 1988; Peart 1989a; D'Antonio and Corbin, unpublished data). Foin and Hektner (1988) documented the replacement of annual species with exotic perennial grasses at Sea Ranch following the cessation of grazing, a process that has been supported by anecdotal observation in such preserves as Bodega Marine Reserve (Sonoma County) and Pt. Reyes National Seashore (Marin County). In these cases, secondary succession toward dominance by perennial grasses is, apparently, the dominant process in ungrazed habitats (Heady 1988), while grazing appears to prevent the competitive exclusion of annual grasses and forbs (Hayes and Holl 2003a).

Exotic perennial grasses are also able to invade communities dominated by native perennial grasses. Thomsen (2005) demonstrated that *H. lanatus* successfully invaded established stands of *B. carinatus* and *F. rubra*. In one multi-year sampling of a relatively undisturbed coastal prairie grassland (Tom's Point Preserve in Marin County), D'Antonio and Corbin (unpublished data) found that percent cover of exotic perennial grasses increased from 1999 to 2006. The increase in percent cover was greatest in years with abundant late-season rain.

The invasion of exotic perennial grasses into coastal prairie grasslands raises concerns that even remnant stands, heretofore resistant to invasion, may face an uncertain future. Based on their capacity to invade natural communities and their impacts on intact communities, *F. arundinacea*, *H. lanatus*, and *P. aquatica* were classified as a "medium" threat in the 2006 California Invasive Plant Council's (Cal-IPC) Invasive Plant Inventory (Cal-IPC 2006). This ranking is on a par with

that of exotic annual grasses such as *Avena* spp., *B. diandrus*, and *Lolium multiflorum*. Of particular concern is the fact that these exotic perennial grasses are likely still expanding and have the potential to impact ecosystems dominated by both exotic annual grasses and native perennial grasses. Future research should examine the potential spread and impacts of these relatively recent invaders.

Perennial Grasses vs. Annual and Perennial Forbs

Because of the scenic and biodiversity value of native forbs in coastal prairie grasslands (Heady et al. 1988), there has been increasing interest in management strategies that control annual grass growth and maximize forb diversity (Hayes and Holl 2003a). Principle among these strategies is the use of grazing that can control grass growth and that is capable of excluding annual and perennial forbs (Chapter 17). Foin and Hektner (1986) found that succession following the cessation of grazing led to a twofold decrease in the cover of annual and perennial forbs and a similar increase in perennial grasses (mostly exotic) in two Sea Ranch (Mendocino County) grasslands. Hayes and Holl (2003a), comparing paired grazed and ungrazed sites along the central and northern coast, found that native annual forb species' richness and cover were over two-fold higher in grazed sites than in ungrazed sites. However, grazing had negative impacts on native perennial forbs.

Recent evidence has suggested that perennial grasses, including *N. pulchra*, are competitive against taprooted forb species such as the invasive weed *Centaurea solstitialis* (yellow starthistle). Reever Morghan and Rice (2005) reported reduced survival and growth of yellow starthistle as *N. pulchra* stands matured. By contrast, yellow starthistle is able to effectively invade stands dominated by annual grasses, perhaps because of abundant soil moisture below the rooting zone of annual grasses (Enloe et al. 2004). Native perennial grasses, with their deeper rooting profiles, reduce soil moisture deep in the soil profile to a greater extent than exotic annual grasses (Enloe et al. 2004; Gerlach 2004). Thus, the invasion of California's Central Valley grasslands by annual grasses may have left deep soil moisture resources untouched and promoted the invasion of these sites by deep-rooting species such as *C. solstitialis* (Chapter 7).

Specialized Competitive Situations—Edaphic Sites

SERPENTINE SOILS

Serpentine communities are dominated by annual grasses and herbs and tend to be very resistant to invasion. The soil characteristics create physiologically harsh growing conditions but support diverse communities with a relatively high proportion of endemic species (Harrison and Viers, Chapter 12; Kruckeberg 1984). Productivity is much lower than in surrounding soils, and water is likely very limiting and is probably a function of soil texture (Harrison 1999a). Very few

non-native species have invaded these communities, but the exceptions are notable. Harrison (1999a) documented 33 alien species in her sites, and soil nitrate was a significant predictor of invasive diversity. *Aegilops triuncialis* (barbed goatgrass) is common on these soils throughout northern California and is often a dominant species. Its ability to invade serpentine has been linked to high phenotypic plasticity rather than adaptation to the stressful conditions (McKay et al., unpublished data). Other non-native annual grasses do not readily invade serpentine patches, but *B. hordeaceus* and *A. fatua* were more likely to be found in small patches than large ones and this was attributed to higher propagule pressure leading to faster selection for serpentine-tolerance (Harrison et al. 2001).

Recently, nutrient inputs from atmospheric deposition have increased nutrient availability, particularly nitrogen, in some serpentine grasslands (Fenn et al. 2003b). As a result, exotic grasses such as *B. hordeaceus* and *Lolium multiflorum* (Italian ryegrass) have successfully invaded previously native-dominated serpentine grasslands (Weiss 1999). As atmospheric nitrogen deposition continues across large areas of California, the unique species composition of some serpentine grasslands may shift.

VERNAL POOLS

Vernal pools are shallow seasonal wetlands fed by rainwater and are perched on impermeable clay soils, often with low nutrient availability and low pH. The highly diverse communities are very resistant to invasion by aliens. Holland and Jain (1988) estimated non-natives at 7% of the species, and a recent survey by Michael Barbour and colleagues confirmed that aliens remain at or below 10%, despite the fact that aliens often comprised 90% of the biomass of surrounding grasslands. Establishment and survival in vernal pools is more likely driven by stress tolerance than by resource competition, because species must germinate in the winter while inundated but mature in hot and dry conditions. Resource competition is likely dominated by water and only for a very short period in late spring, depending on the rainfall patterns of the particular year. Native species mature as the water level recedes, and each species can be characteristic of particular zones around the pool. It is very likely that the combination of fluctuating water resources, edaphic stress, and well-adapted natives may limit non-native invasions in vernal pools except by preadapted species from similar habitats.

Life History Characteristics

The components of California grassland communities employ very different strategies—including variation in lifespan, summertime activity, rooting patterns, and allocation to root vs. shoot tissue—to survive the conditions of California's Mediterranean climate and its annual summer drought. A comparison of the life-history characteristics of annual and

perennial species, with an eye toward understanding how differences between various groups—annual grasses, perennial grasses and forbs—influence species composition in various grassland habitat types is useful.

Longevity

As previously noted, annual species germinate quickly with the arrival of sufficient rainfall in the fall and complete their entire life-cycle—germination, growth and reproduction—by the time the rains have tapered off in the spring and summer. By contrast, perennial species invest in root systems that allow them to survive the summer drought and live, in some cases, for decades.

The difference in longevity between annuals and perennials means that they have fundamentally different approaches to the early stages of growth. Annual plants, for the most part, germinate and grow quickly, investing mostly in above-ground biomass and reproductive structures compared to roots. Perennials, on the other hand, are frequently more conservative in terms of resource use and have slower growth rates. Reynolds et al. (2001), using seeds grown in growth chambers, found that seeds of exotic annual species germinated as much as 1–2 weeks earlier than native or exotic perennial species. This two-week advantage may provide the annual seedlings a considerable advantage vs. perennial seedlings: Biomass of the native perennials *Nassella pulchra* and *Festuca rubra* and the exotic perennial *Holcus lanatus* was significantly greater when their seeds were allowed to germinate 14 days before seeds of *B. diandrus*, as compared to treatments in which the perennial and annual seeds were allowed to germinate at the same time (Abraham et al., unpublished data).

The rapid growth of winter annuals in late spring exacerbates the resource stress experienced by perennial grasses, especially at the seedling stage. For example, depending on soil characteristics, moisture depletion in the upper 60 centimeters occurs earlier in the season when annuals are present (Gordon and Rice 1992; Brown et al. 1998; Dyer and Rice 1999). The diffuse competitive effect of thousands of annual plants per square meter amplifies resource stress at the habitat scale (Dyer and Rice 1997b).

The longer lifespans of perennial species may give them an advantage over annual species once the perennials are mature. Several studies have reported a correlation between bunchgrass size (or age) and resistance to invasion by annuals (Brown et al. 1998; Hamilton et al. 1999; Corbin and D'Antonio 2004b; Reeve Morghan and Rice 2005). Corbin and D'Antonio (2004b) argued that the ability of perennial species to hold onto space and resources over the summer gave them the advantage of “incumbency” over newly germinating annual species. This mechanism may be especially important in coastal habitats, where perennial grasses maintain biological activity well into the summer, as compared to inland habitats, and therefore can occupy a substantial proportion of resources as the fall rains begin.

Summer Activity

One of the most obvious differences between the life history strategies of annual and perennial species is the senescence of annual species prior to the onset of the summer drought. In effect, populations of annual species, including the dominant annual grasses, *survive* the summer drought as seeds in or on the soil. In contrast, many perennial species are metabolically active during the summer drought and often have at least some green tissue.

Where summertime inputs of moisture are low or absent (e.g., all but the most maritime conditions along the coasts), perennial species survive the drought by utilizing residual soil moisture left over from the wet season. Perennial grasses and taprooted perennial forbs develop root systems that take up water as deep as 50–100 cm below the soil surface (Holmes and Rice 1996; Enloe et al. 2004). Competitive pressure from annual species during the winter and spring may negatively affect the ability of perennial species to reach belowground resources during the summer (Dyer and Rice 1999; Hamilton et al. 1999).

Availability of summer moisture, and the ability to use it, is a critical difference between inland and coastal grasslands. Corbin et al. (2005) found that fog was a significant summer water source in coastal grasslands—25–66% of the water in perennial grass tissues derived from fog as opposed to residual rainwater. The ability to use fog water suggests that coastal grass roots are continuously active in the shallow soil profile, even during the summer (Corbin et al. 2005). This pattern stands in stark contrast to the reliance on deep soil moisture by inland perennial grasses (Dyer and Rice 1999; Brown et al. 1998). Inland grasslands experience occasional summer showers, but there is little empirical evidence on the extent to which perennial grasses make use of such ephemeral resources. Experimental rainfall studies with *Agropyron desertorum* in the Great Basin found either no new root growth (Ivans et al. 2003) or a three day lag after the rain event (Cui and Caldwell 1997).

Summer moisture provides a mechanism to explain why perennial grasses can dominate coastal grasslands but not inland grasslands. Dominance in this case is not necessarily through superior competitive ability for water, but by site pre-emption via continued growth after annual species have become senescent—i.e., through a different phenology that better allows the capture of the late season water not available in inland grasslands. Unfortunately, in coastal grasslands, the conditions that favor native perennial grasses also favor exotic perennial grass, and therefore summer moisture may decrease invasion resistance to those taxa (Corbin et al. 2005).

Rooting Patterns

Annual grasses deploy 90% of their roots in the upper 30 centimeters of the soil profile (Holmes and Rice 1996) and greatly reduce soil water in that zone (Seabloom et al. 2003b). In contrast, perennial grasses begin their life with roots in the topsoil, but large individuals root to 1.5m or more in deep

soil (Dyer and Rice 1999; Brown et al. 1998). Therefore, in deep soils perennial grasses can partition soil resources vertically and avoid much competition with annuals in the upper 30cm. In shallow soils, however, annual and perennial grasses compete for the same soil resources (Dyer and Rice 1999; Seabloom et al. 2003b).

In perhaps the most extensive study on native grasses to date, Brown et al. (1998) investigated the links between resource partitioning and capture, species composition, and age of stand. By creating a variety of experimental swards with up to seven species of native perennial grass, they were able to look at water use, biomass production, and response to non-native annuals over the course of consecutive growing seasons. *N. pulchra* individuals in containers were capable of reducing soil water to a significantly greater degree and at greater depths than other native grasses. In field experiments, summer-active native perennial grasses deployed much greater proportions of their roots to deeper soil layers compared to annual grasses. Cool-season perennial grasses tended to have similar root profiles compared to annual grasses. These data support the contention that root establishment is critical if perennial grasses are to survive the seasonal drought. Overall, this series of experiments demonstrated that established perennial grasses can be very competitive for water, but also that the conditions in exotic annual communities limit the ability of perennial grass seedlings to capture resources and grow.

These differences in rooting patterns likely influence susceptibility to growing season droughts. Evidence from experimental (Hamilton et al. 1999; Sher et al. 2004) and observational (Pitt and Heady 1978) studies suggest that annual grasses are especially sensitive to periods of drought during the winter and may be poor competitors for water when this resource is scarce. Annual grasses do not develop deep root systems that can reach deeper sources of water (Holmes and Rice 1996) and likely can grow only when abundant moisture is available. By contrast, perennial species develop deeper root systems (Dyer and Rice 1999; Enloe et al. 2004) and are adapted to survive even extended droughts, such as those that occur during the summer months.

In an experimental test of the relative impacts of a growing-season drought on annual and perennial grasses, Hamilton et al. (1999) found that a simulated drought (35 days) in December and early January decreased the biomass of exotic annual grasses by more than 25%, while survival and biomass of *N. pulchra* seedlings were not affected. In a study using two annuals—*V. myuros* and *Erodium laciniatum* from the Mediterranean-climate region of Israel—Sher et al. (2004) found that these species were sensitive to increasing lengths of growing-season droughts. Increasing the length of time between rainfall events decreased relative growth rate and survival of both annual species at low (100 mm/season) and high (500 mm/season) water regimes. Yet periods without precipitation are regular features of California's climate, even during the winter. Null (2006), using climate records from San Francisco, reported that dry spells of at least 8 days (mean

duration = 19 days) during December and January occurred every year from 1950–2005.

These results indicate that competition for water in California resembles the “two-phase resource dynamics” hypothesis (Goldberg and Novoplansky 1997). According to this hypothesis, availability of a resource such as water can be divided into periods when the resource is plentiful (or “pulses”) and periods when it is too scarce for plant growth (“interpulses”). While competition may be most intense during resource pulses in productive environments, interpulses may be the most important environmental factor for plant growth and survival in unproductive environments (see discussion of serpentine and vernal pool communities in previous paragraphs). In Mediterranean climates such as California, distinct pulses and interpulses occur within each growing season as well as between the distinct winter pulse period and the summer interpulse period. Pulses and interpulses may occur several times within a growing season as precipitation may be absent for 1–3 week periods (Null 2006). Thus, competition dynamics in annual grasslands—even during the winter—may be as much a function of the frequency and duration of dry periods as it is the availability of water during periods when water is plentiful.

Aboveground Productivity

Perennial grass seedlings and small-statured plants are highly susceptible to light limitation by the dense and taller annual neighborhood. Dyer and Rice (1999) found that light penetration in exotic annual grass-dominated plots at Jepson Prairie (Solano County) was as low as 5% of full sun. Of course, reduced light availability greatly slows vegetative growth, thereby making the perennial grass progressively less able to compete for light. Reduced carbon fixation also reduces absolute allocation to roots. By late spring or early summer, the surviving small perennial-grass individuals are ill-prepared for the summer drought. Thus, competition with annuals for light in early spring reduces the root growth necessary for survival through the annual summer drought.

The story is almost exactly reversed when competition between established perennial grasses and annual grasses is observed. Corbin and D’Antonio (2004b) and Seabloom et al. (2003b) concluded that the ability of the perennials to reduce light available for exotic annual grass seedlings reduced exotic productivity and maintained perennial dominance. Similar results were reported for the effect of *N. pulchra* on the survival and growth of *Centaurea solstitialis* (Reever Morghan and Rice 2005).

Regardless of the location of the grassland, light limitation is a function of productivity and this, of course, is closely linked to water availability and soil quality. Thus, light limitation is likely to vary temporally and spatially. In years when climatic conditions are favorable for exotic annual growth (e.g., “grass years,” *sensu* Pitt and Heady 1978), or in richer soils that can support greater productivity, light limitation should

be greater and should occur earlier in the growing season. In such systems, space acquisition (e.g., rosette formation) and vertical growth should be favored. In less favorable years or in resource-poorer systems, light is less likely to be a limiting factor because of reduced annual grass productivity.

Nitrogen Use

The uptake of inorganic N by vegetation during the growing season keeps pool sizes of KCl-extractable inorganic N ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) small (Eviner and Firestone, Chapter 8; Jackson et al. 1988; Corbin and D’Antonio, 2004a). Though evidence is scarce, it is likely that elevated N levels favor exotic annual grasses more than other components of grassland communities. N fertilization frequently increases productivity in California grasslands (Harpole et al., Chapter 10) and is capable of shifting species composition in serpentine and non-serpentine grasslands toward exotic annual grasses (Huenneke et al. 1990, Weiss 1999, Seabloom et al. 2003b). However, the extent to which species composition of non-serpentine-derived soils varies along gradients of soil fertility is not clear. In one of the few studies documenting community changes following N addition to nonserpentine grassland, Seabloom et al. (2003b) found that *N. pulchra* cover decreased over 5 years of fertilization. However, there was no corresponding increase in other community components that would suggest a role for competitive interactions.

The invasion of N-fixing shrubs such as *Lupinus arboreus* into coastal prairie grasslands provides a natural experiment showing the effects of nitrogen on grassland community composition. *L. arboreus* shrubs, which grow rapidly and produce a dense canopy that shades out native grassland species, are capable of reducing native plant diversity and increasing dominance by annual species. Maron and colleagues (Maron and Connors 1996; Maron and Jefferies 1999) demonstrated that repeated cycles of lupine colonization and death led to a doubling of total soil N, greatly increased N availability, and increased vegetative productivity. These cycles caused a large-scale shift in grassland composition from native perennial to exotic annual species, presumably due to the greater responsiveness of annual species to the elevated N levels than perennial species.

Several efforts to favor native perennial species in a restoration context by reducing plant-available N have not altered species diversity or dominance. Addition of a labile carbon source, such as sucrose or sawdust, would be expected to stimulate production by C-limited microbial populations and to reduce plant-available nitrogen. Addition of sucrose and sawdust has been attempted in coastal prairies in an effort to reduce productivity of exotic species and increase native biodiversity (Alpert and Maron 2000; Haubensak 2001; Corbin and D’Antonio 2004a; Corbin et al. 2004). However, even where these efforts have been successful at reducing exotic abundance or productivity (Alpert and Maron 2000), they have not resulted in a change in competitive outcomes between annuals and perennials.

Relatively few studies have experimentally tested the role of N in competitive interactions in California grasslands (Huenneke et al. 1990). Differential abilities to grow under N-limited conditions have been shown to play an important role in determining the outcome of competitive outcomes in other grassland systems (Tilman 1988), and it is suspected that the same is true in California systems. To date, however, the ability to predict interactions of competitive outcomes under various N levels is limited. Further research is needed in this area as elevated N inputs from atmospheric N deposition have the potential to increase N availability to grasslands throughout the state (Weiss 1999; Fenn et al. 2003b).

Physical Barriers

The accumulation of plant litter has been shown to influence seed germination rates and species composition in a variety of North American grasslands (Heady 1958; Young et al. 1971; Hamrick and Lee 1987; Facelli and Pickett 1991a, b; Foster and Gross 1998; Reynolds et al. 2001). The presence of litter in California grasslands has been shown to have a positive effect on seed germination rates (Young et al. 1971), presumably by increasing moisture retention at the soil surface (Facelli and Pickett 1991b). However, litter accumulation can also form a physical barrier that limits establishment of germinating seeds (Reynolds et al. 2001). Responses to the presence of litter varies by species (Young et al. 1971; Reynolds et al. 2001), and thus the presence and abundance of litter is likely to influence community composition.

Management strategies such as prescribed burning and grazing have been widely applied in efforts to reduce negative effects that litter accumulation can have on native grass and forb germination and establishment (Chapter 17; Reiner, Chapter 18). However, fire and grazing can alter environmental conditions or competition in a variety of ways, including reducing litter accumulation but also mortality, productivity, and allocation to roots vs. shoots, and it has not been easy to quantify the precise effects of each treatment type. As a result, the mechanisms by which these treatments may affect native seed germination or establishment have been difficult to quantify.

Management Strategies to Alter Competitive Outcomes

The re-establishment of populations of native species in habitats from which they have been eliminated is of tremendous practical importance. Indeed, it is the focus of the multimillion-dollar restoration efforts taking place in grasslands throughout California (Stromberg et al., Chapter 21). No less important are the theoretical implications to understanding population dynamics and community interactions. The low density or even absences of native species in the vast majority of grasslands (Heady 1988; Stromberg et al. 2001) is the net result of many ecological factors operating across the spatial and temporal scales that govern population sizes including seed dispersal, fecundity, competitive ability, and

response to disturbances (Stromberg and Griffin 1996). Recent research has turned to ways of influencing competitive relationships between native and exotic species through active management in an effort to achieve management goals such as increased native biodiversity (Corbin et al. 2004).

Grazing

The grazing of cows, sheep, and goats has been widely applied in an effort to influence competitive outcomes and favor one group of species over another (e.g., native vs. exotic species). Huntsinger et al. (Chapter 20) provide a detailed review of the application of grazing in the promotion of native biodiversity. In theory, specifically timed grazing regimes could capitalize on differences in phenology to promote desirable species (Augustine and McNaughton 1998). However, although some experimental studies have demonstrated the effectiveness of grazing in influencing competitive outcomes and promoting native biodiversity (Love 1944; Langstroth 1991; Dyer et al. 1996; Hayes and Holl 2003a; Marty 2005), the benefits are by no means universal (Chapter 20) and are sometimes short-lived (Dyer et al. 1996). Huntsinger et al. (Chapter 20) conclude that in the absence of more carefully designed tests of the impacts of grazing on competitive outcomes between native and exotic species, site-specific factors, including the species pool, land use history, and climate, make generalizations difficult.

Fire

Prescribed burning has also been used in an effort to manage grasslands, particularly in the control of exotic species and the restoration of native biodiversity (Reiner, Chapter 18). Fire has the potential to alter competitive interactions because of its effects on standing vegetation, residual litter, seed survival, and seed germination. It can also substantially alter growing conditions by altering nitrogen and light availability (Chapter 18). To date, however, the effects of fire on the competitive interactions between various groups of species (e.g., annual grasses versus perennial grasses) has not been examined.

Seed Addition

Any discussion of the difficulty of reestablishing native populations in exotic-dominated habitats must begin with the low supply of seeds reaching appropriate habitats. The paucity of individual native grasses or forbs that produce viable seeds in many grasslands means that seed availability is a primary factor limiting native population growth rates (Baker 1989; Hamilton et al. 1999; Seabloom et al. 2003b). Even in grasslands where native species persist, native seedling recruitment is generally very low (Bartolome and Gemmill 1981). Experimental evidence has shown that artificial increases in seed supply increase the density and cover of native grasses and forbs. Hamilton et al. (1999) found that *N. pulchra* seedling density was five times higher in plots that received seed addition (5,000 seeds per m²) than in plots that did not.

Seabloom et al. (2003b) found that percent cover of perennial grasses (*Bromus carinatus*, *Elymus glaucus*, *Nassella cernua*, *N. pulchra*, and *Poa secunda*) increased in previously disked annual-dominated old-field communities following seed addition (500 seeds per m²). Seed addition studies using native annual forbs have found many species to be seed-limited in both native- and exotic-dominated grasslands (Robinson et al. 1995; Brown and Bugg 2001; Seabloom et al. 2003b; Gillespie and Allen 2004). A single seeding can lead to persistent increases in population density, although success is often adversely affected by the abundance of grass competitors.

Assessing the degree of seed limitation in perennial species is complex because the expected lifetime fecundity of establishing individuals must be factored into any estimate of population growth rate. This is experimentally intractable for species, such as perennial grasses, that can live for decades or centuries. In lieu of direct measurements, we constructed a simple matrix model that evaluates long-term population growth rates (λ) from short-term seed addition experiments (Box 13.1; Table 13.2).

We based our estimates of seedling survival (p_{12}) on seven studies in which native perennial grasses were seeded into intact grasslands and tracked through their first year (Table 13.2). These studies were conducted in six different years and three counties spanning a twofold rainfall gradient from Santa Barbara County (~350 mm) to Yolo County (~650 mm). Survival ranged from 0–9% (median 6.6%) and did not differ significantly whether seeds were added to annual- or perennial-dominated grasslands (Table 13.2).

Our matrix model projections show that perennial grasses with a mean lifespan of at least 5 years should have positive population growth rates in 75% of empirical trials (Box 13.1; Figure 13.3). The two studies with the lowest seedling survival were replicated in subsequent years (Robinson 1971, Dyer et al. 1996). It is interesting to note that in both cases, seedling survival was sufficient for positive population growth rates in one of the years and probably insufficient in the other. In fact, Robinson (1971) measured the second highest (39%) and lowest (0%) survival rates in consecutive years at the same site. This high interannual variability suggests that seedling success is driven more by temporal than spatial variability. There are more likely to be good and bad years for seedling establishment than specific locations where seeds can never establish. This result suggests that multiple reseedings may be necessary to establish perennial grass populations.

Population growth rates were sensitive to survival through the first year (p_{12}), confirming the assumption that early survival represents a major bottleneck for perennial grass restoration. Population growth rates increased with adult lifespan (p_{34}), although the effects were much less pronounced than those of survival through the first year (p_{12}). Population growth rates were relatively insensitive to adult fecundity (f_{31}), survival through year 2 (p_{23}), and adult survival (p_{34}). The model did not include density-dependent interactions, including interspecific competition, that are likely to occur after establishment.

Competition with annuals at the seedling stage has also been consistently implicated in the failure of perennial grass establishment. Indeed, once a seed reaches an appropriate habitat and germinates, the seedling must still compete with neighbors for resources before it can successfully establish and survive. In many invaded grasslands, dense stands of exotic annual seedlings restrict the access of native seedlings to light and belowground resources (see previous sections) (Langstroth 1991; Dyer et al. 1996; Hamilton et al. 1999; Brown and Rice 2000). Thus, competitive interactions likely limit establishment of native species in most exotic-dominated grasslands, perhaps in concert with seed limitation.

Divittorio et al. (in press) suggested that existence of seed limitation of native species may be controlled by the density of exotic competitors. Using correlations between seed rain (native and exotic) and the establishment of native seedlings on experimental disturbances, they concluded that seed limitation of native species existed only when exotic seed supply and resulting interspecific competition was low. Even though native populations in exotic-dominated grasslands may respond to increases in seed supply because of low abundances of (native) reproductive individuals, the presence of numerous exotic seedlings likely shifts limitation to competition (Divittorio et al. 2007). This is similar to the conclusions of Hamilton et al. (1999) in that recruitment of *N. pulchra* was seed limited because of reduced local abundance, but competition for water was ultimately a stronger factor limiting the potential for native population growth.

It is suspected that the rate of increase of native grass populations in many habitats is co-limited by both seed limitation and seedling competition. Treatments that overcome one limitation without considering the other are likely to be relatively unsuccessful. In contrast, restoration strategies that simultaneously increase the supply of native propagules (Box 13.1) while also reducing the competitiveness of exotic competitors are likely to be most effective (Chapter 21; Corbin et al. 2004). Further investigations that test the interactions between native seed addition and treatments that reduce exotic competitiveness, such as herbicide, grazing, or solarization, will help determine the relationship between factors limiting native establishment.

Summary

Competitive interactions play an important role in determining the species composition and relative abundances of plant species in California grasslands. The dominance of exotic annual grasses, particularly in interior regions of the state, suggests that they are superior competitors versus perennial grasses and annual and perennial forbs under a variety of settings. The ability of annual grasses to germinate quickly, and their ability to effectively deplete soil moisture and light available to other types of vegetation, are some of the mechanisms that have been suggested to explain the annuals' success. Perennial species, including both native and exotic grasses, fare better in

competition with annual grasses in coastal habitats, where greater moisture availability during the summer drought leads to a longer growing season. Once established, perennial species in these coastal habitats have been shown to be able to significantly reduce growth of exotic annual competitors.

Management strategies—including grazing, prescribed fire, and seed addition—have been applied in an effort to influence competitive outcomes in favor of native species. Thus far, no single strategy has proven successful in reducing the competitiveness of exotic species across a range of habitats. Most likely, a mixture of methods that includes the addition of native seeds along with treatments such as grazing or burning

that are designed to reduce competitors' growth and survival will have the greatest likelihood of increasing native establishment and survival. Future research should examine such multiple strategies, while specifically addressing mechanisms that are likely to drive changes in competitive interactions between native and exotic species.

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